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A REVIEW OF THE NATURAL HISTORY OF THE MARSHALL ISLANDS

BY

F. RAYMOND FOSBERG

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A REVIEW OF THE NATURAL HISTORY

OF THE MARSHALL ISLANDS

BY

F. RAYMOND FOSBERG

This review was prepared on very short notice, to provide a summary of what is known to the reviewer at the time, June 1988, about the natural phenomena of the Marshall Islands. This was for the use of the members of the survay team sent to the Marshalls by the Environmentand Policy Institute of the East-West Center, Honolulu. Their mission was to investigate the remaining relatively natural areas and the extent of biodiversity in the new Republic of the Marshall Islands.

The Marshall Archipelago has been the habitat of Aboriginal man for many hundreds, perhaps even thousands, of years. Hence there is very little, if any, undisturbed land remaining.

Since the coming of the Europeans, in the 19th Century, and especially in the years 1940 to the present, the disturbance and change have been greatly intensified. On four of the Atolls, namely, Eniwetok, Bikini, Kwajalein, and Majuro, the alteration has been catastrophic. Change is so rapid that even a superficial account of what was observed during the early and mid 1950's seems worth placing on permanent record.

This account is definitely not the results of a systematic literature search, but merely what is stores in the reviewer's head and in his notebooks, with such additions as are acknowkedged in the text. The account has been slightly, but not thoroughly, edited for more general publication, but its semi-popular level has not been changed, nor have all references to the Survay been deleted.

ACKNOWLEDGEMENT

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Contents

INTRODUCTION

This compilation is intended to summarize the physical geography and natural history of the Marshall Islands, explaining the natural features and diversity in these islands as they form the environment of the human populations found there - the Marshallese people.

Emphasis is on the natural environment, only briefly describing those environmental features resulting from human activities. The purpose is to explain the natural diversity in this environment and make possible an understanding of the influence of this diversity on the evolution and nature of the indigenous Marshallese culture, and to indicate such areas as still show viable examples of these features, after perhaps several thousand years of changes wrought by this culture, itself, and a hundred and fifty years of accelerated change under the increasing influence of Western European (including American) influence. In the past few years there has been an abrupt popular awakening of the importance of preserving and maintaining as much as practical of the natural diversity in the human environment.

Realization of this importance has led to a request for scientific advice as to the location and nature of the remaining areas of relatively unaltered environments in the Marshalls. This summary is intended to serve as background data to guide field investigations to determine the present extent and status of areas that may be worthy of selection as protected areas.

In order to serve both the field investigators sent out by the Environment and Policy Institute of the East-West Center, and perhaps cooperating agencies, and the Marshallese policy-makers, the language is deliberately less technical than might be necessary for strictly scientific communication and background information. It also may include material that might seem obvious and unnecessary to the scientific users. Its scope is perhaps overly limited by the extent and knowledge of and familiarity with the islands and the intention of the compiler. If this results in omission of material of importance, the users have his apologies. Certain geographical items, peripheral to the main purposes of this compilation, and the names of some animals that may be rare or endangered are not readily available, or would necessitate time-consuming research. Hence there may be gaps that would not be tolerable in a paper originally intended for scientific publication. The details in the descriptions of Wotho Atoll, transcribed with some editing, from the compilers field notes may seem excessive, but since it amy be the only available detail description of moist, semi-natural coral atoll

recorded in the field, it seems of enough value to be placed on record and made available as a "base-line".

References are listed that may provide more complete information than is included here.

GEOGRAPHY

The newly founded Republic of the Marshall Islands consists of 29 atolls and 5 small islands or "table-reefs," lying in the inner angle of the Northwest quadrant of the Pacific Ocean, North of the Equator and West of the 180° meridian. West of this stretches the Caroline Archipelago, South of it the Gilbert Islands (Kiribati).

Tha Marshall Archipelago is about 1300 km E-W, 1150 km N-S, scattered irregularly in two vaguely defined chains, the Ralik, or western, and Radak, or eastern, trending somewhat Northwest to Southeast. The atolls and islands are listed in the two chains in Table 1. Exact areas for some of the atolls and islands are not readily available. The total land area is said to be about 70 square miles, while the total area including lagoon is about 4507 square miles.

All are low coral islands, made up, geologically speaking, entirely of calcium carbonate in the form of "coral sand and gravel," of cobbles and boulders, and of consolidated limestone - slightly elevated reef in growth position, consolidated limestone debris (platform), and beach-rock. The shore-line is formed by coral-sand -, gravel -, and boulder -, beaches, beach- rock, and "erosion ramps" - sloping zones of eroded platform rock, often corrugated perpendicularly to the edge of the sea. Locally are low (1 m) undercut intertidal cliffs, either in unconsolidated sediment or in platform rock.

Table 1. - Lists of the two chains of the Marshall Archipelago.

Ralik Chain		Radak Chain	
Eniwetok Atoll	2.22 sq. mi.	Pokak (Taongi) Atoll	1.45 sq. mi.
Ujelang Atoll	0.62 sq. mi.	Bikar Atoll	0.19 sq. mi.
Bikini Atoll	2.82 sq. mi.	Utirik Atoll	1.04 sq. mi.
Ailingcnae Atoll	1.29 sq. mi.	Taka Atoll	0.22 sq. mi.
Rongelap Atoll	3.07 sq. mi.	Ailuk Atoll	2.19 sq. mi.

Rongerik Atoll	0.81 sq. mi.	Mejit Island	1.32 sq. mi.
Wotho Atoll	1.60 sq. mi.	Likiep Atoll	3.9 sq. mi.
Ujae Atoll	0.62 sq. mi.	Jemo Island	0.07 sq. mi.
Lae Atoll	0.60 sq. mi.	Wotje Atoll	3.16 sq. mi.
Kwajalein Atoll	6.33 sq. mi.	Erikub Atoll	0.35 sq. mi.
Lib Island	0.36 sq. mi.	Maloelap Atoll	3.69 sq. mi.
Namu Atoll	2.42 sq. mi.	Aur Atoll	2.17 sq. mi.
Jabwot Island	0.22 sq. mi.	Majuro Atoll	3.54 sq. mi.
Ailinglapalap Atoll	4.67 sq. mi.	Arno Atoll	5.00 sq. mi.
Namorik Atoll	1.07 sq. mi.	Mili Atoll	5.77 sq. mi.
Kili Island	0.36 sq. mi.	Knox Atoll	0.38 sq. mi.
Jaluit Atoll	4.38 sq. mi.	Ebon Atoll	2.22 sq. mi.

Extending outward from the shore for varying distances are "reef-platforms" - flat smooth planation (or possibly growth) surfaces, ending seaward either in an abrupt drop-off on leeward sides of atolls or, on windward sides, in a low trough or moat contained by a definite ridge, which may rise a meter or more above mean sea-level, then a steep drop-off to deep water.

For the benefit of possibly less well-informed users it may be advisable to briefly explain what is meant by the term "reef" or "coral-reef" frequently used in this account. A coral-reef is a living (or formerly living) community of a multiplicity of marine organisms, plants and animals, the structurally important ones of which secrete skeletons of calcium carbonate, or limestone. Certain of these, especially corals and encrusting calcareous red algae, tend to fuse together to form massive stony lattice-works and rigid solid structures, often of enormous extent, in relatively shallow areas of ocean, especially along and near coastal land. Additionally, myriads of species, again of both plants and animals, form particulate skeletons - shells, tests, small plates and flakes, spicules, and spines, all of which accumulate after death of the organisms, to form sediments. These, with pieces of larger skeletons broken by waves and other forces, undigested limey matter excreted or dropped by eaters of the owners of

the skeletons, form vast quantities of calcareous debris which fill the interstices of the reef-lattice and depressions in the surfaces. Consolidation by cementation and by growth of encrusting organisms, of these lattices and sediments forms what are known as coral-reefs, and which are seen as spectacular and often incredibly beautiful phenomena in shallow tropical seas. These also form habitats and hiding places for myriads of softer species of plants and animals which are also members of these living communities.

The term atoll, strictly speaking, refers to a usually irregularly ring-shaped reef with one to many "islets", areas above high tide level, lying on it. This reef-ring encloses a (usually) sea-water lake or "lagoon," connected, in most cases, with the sea by one or more deep channels or "passes" and/or by small shallow channels called (in the Tuamotu language) "hoa."

On most islets just inland from the top of a beach or hard-rock shore, lies a low (usually 1-2 m) ridge of sand or gravel called a beach ridge. These ridges are much less well-developed, or even absent, on lagoon-sides of islets. Occasional stretches of beach-ridge, have cobbles and even boulders of coral limestone, in some places piled up forming higher ridges to even 5-8 (-10) m, considered to have been thrown up by storms or hurricanes. In some places there are several concentrically parallel such ridges, the older ones inland, the newer or fresher ones seaward, representing several storms. Occasional huge blocks or boulders are found well-inland, apparently thrown there by tsunamis ("tidal waves") or by hurricane waves.

The interior of most islets is low, flat and sandy. Seaward the texture may become coarser, and areas of exposed lithified breccia or conglomerate occur, probably formed during a post-glacial warm period with higher sea-level. The material of this structure, reef plus islets, is entirely of calcium carbonate, except for occasional pebbles of pumice, thrown up on the beaches by waves after floating from far-away volcanoes, perhaps such as Krakatau. Occasional bones of turtles and even whales may be found, buried or exposed.

The terms "coral," "coral-sand," "coral-rock," or "coral limestone" are general ones, referring to limestone materials of various textures and degrees of lithification, of organic origin, and comprising in addition to true corals, calcareous algae, foraminiferal tests, mollusk shells, sponge spicules, and fine unidentifiable triturated, precipitated, or crystalline calcium - or calcium magnesium carbonate. Inland, in addition to such carbonate materials, are occasionally found beds of lithified calcium phosphate

or "atoll phosphate rock" (discussed at greater length below).

GEOLOGICAL ORIGIN OF ATOLLS

The curious ring-shaped arrangement of atoll reefs has long excited the curiosity of observers - geographers, geologists, biologists, and interested laymen, alike. Much has been written on the subject, a literature far too extensive to summarize here. Suffice it to say that an idea first suggested by Charles Darwin well over a century ago, and gradually confirmed since amid much controversy, has developed to a concensus among qualified workers in all of the above scientific disciplines. This, expressed here very briefly, maintains that oceanic coral atolls began as volcanic islands, around which fringing coral reefs formed. This was followed by extremely slow subsidence, either isostatic or tectonic of the volcano or its remnants. Coral and algal growth is much more rapid in the turbulence zone on the seaward edges of the reefs, resulting in these outer edges keeping up with the rate of subsidence, while the slower growing inner areas become submerged. Such shallow water areas are termed "lagoons.* This slowness of growth may be contributed to by fresh water and silt draining from the land, not favoring many of the organisms living in lagoons. Many lagoon organisms, such as sea-grasses, also do not have calcareous skeletons, hence do not contribute material for upward growth of lagoon floors.

The loose sediments that occur on reef surfaces, especially in rough weather, and especially in storms and hurricanes, tend to be piled up as sand-bars on the reef surfaces. These tend to shift with waves and currents, but some surfaces are exposed above high-tide level. Also, in the inter-tidal zones of beaches not-altogether-understood process forms consolidated, outward sloping beds of rock called "beach-rock." This tends to stabilize these bars. Terrestrial plants gain footholds, forming salt-resistent vegetation, which holds the loose sediments together, lessening both wind and water erosion. Sand islets or cays are thus formed. Another process, formerly subject of much controversy, is eustatic (world-wide) fluctuation of sea-level. It seems well established that a few thousand years ago during a post-glacial warm period, melting occurred on the world's ice-caps and glaciers, resulting in a 2-meter or more rise over the present sea-level. This allowed reefs to grow to somewhat above their present elevation. Sand cays would have formed on these higher surfaces. With world-wide cooling, or other conditions leading to increase in ice-caps and glaciers, the sea-level receded downward. This not only favored the persistence of the sand-islets but left consolidated reef-rock and beach-rock lying as much as 2

meters above present sea level. Many islets in Marshall Island atolls are partly constructed of platforms of limestone as well as loose sediments.

There is even a suggestion, by traces of still higher limestone on atolls, mostly elsewhere in the world, but also in one locality on Pokak (Taongi), northernmost of the Marshalls, that there may have been an even higher, to 3.5 meters, earlier sea-level. This may have been post-glacial, but the traces may be remnants from higher reefs formed during a warm inter-glacial period before Wisconsin Glacial time.

If the above scenario is well-founded, there may have been a period, not too many millenia ago, when the Marshall Islands were mainly shoals over-washed by waves of the sea. Anyhow, there seems little doubt that the Marshalls were formed by subsidence of ancient volcanoes. Deep drillings, down 1,000+ meters to volcanic bedrock under coral-limestone on Bikini and Eniwetok atolls in the northern Marshalls, have confirmed Darwin's subsidence theory beyond a doubt.

GEOLOGY

A summary of the geology of these atolls will not be attempted here, as such features are covered by geography, soils and hydrology. Geology has only an indirect, though not unimportant, influence on biogeography. Much of what is known is contained in the enbrmous series of accounts in the great series of monographs included in U.S. Geological Survey Professional Paper 260 A-II (Emery et al. 1954 to 1969), in the Military Geography of the Northern Marshall Islands (Fosberg et al. 1956), and in Terrestrial Sediments and Soils of the Northern Marshall Islands (Fosberg and Carroll 1965). Summarizing these and related papers is far beyond the scope of this compilation.

CLIMATE

An account of the Marshall Islands climate adequately dealing with how it fits into and results from the global and Pacific atmospheric circulation, temperature and evaporation patterns, is beyond the scope of this summary. This discussion will be confined only to the tangible or observable results of these patterns which have direct influences on the occurrence and behavior of the organisms that live in and around the islands. And even this much is on a rather superficial level. To do anything further would require a major chapter or even a book-length account, and would delay this summary until its purpose would not be accomplished.

A major restriction on what may be said locally is a

scarcity and spottiness of meteorological records. On only a few atolls these are ample, if not adequate or of long duration. Much of what can be said about the climatic pattern is inferred from the vegetation, and this is limited by the human-caused alteration of the vegetation during the post-European time, essentially the last hundred years. Coconut plantations are not very sensitive indicators of climatic differences.

The striking feature of the regional Marshallese climate is a north-south gradient of increasing rainfall. The northern tier of atolls can be said to have an effectively semi-arid climate. Pokak, the northernmost shows a physiognomy that elsewhere might be considered semi-desert, though its rainfall (unmeasured as yet) may approach that of U.S. western prairie or even Middle Atlantic states. Two or perhaps three factors may contribute to this appearance. Almost perfect drainage due to the porosity of the soil, salt spray and saline ground-water, and probably high evapo-transpiration (generally about 200 mm/year) due to continuous tropical temperatures, and wind are jointly responsible.

Luxuriance, indicating higher and less seasonal rainfall, increases southward to Ebon, southernmost atoll, less than 5o N latitude, which may have had, before alteration, almost a rain forest physiognomy. It is in the equatorial high-rainfall belt. Hence the effects of other climatic variables may be damped or obscured.

A second important climatic feature is the position of the archipelago in the Northeast Trade Wind belt. During the greater part of the year the prevailing winds are from the north-east to the east, and are moisture-laden, though there is no high physiographic relief to bring about orographic dumping of this moisture. Trade-wind showers are frequent except in the northernmost atolls. These winds are also strong enough to carry quantities of salt-spray across the flat expanses of the islands from turbulence at the windward reef margin.

Salinity is an important factor in any atoll situation, especially in drier places where the salt is not washed down into the ground water and flushed out. This salinity has a strong bearing on many natural and human phenomena.

The constantly high, not strongly variable tropical temperatures, influence evaporation, and cold is scarcely a limiting factor on biological activity here.

Finally, tropical storms and hurricanes (locally called typhoons) occur, though not as frequently as farther west. When they occur, they sweep up from the south, exerting

their force from all directions, and pour down great quantities of rainfall. They are strong enough to uproot or break trees and to defoliate and often kill trees that are left standing. No one has even estimated their effects on animal life. Among their conspicuous effects are those caused by their generation of powerful waves that may sweep completely across narrow islets and carry tremendous loads of limestone sediments from the ocean margins onto the land, greatly influencing micro-topography and soil textures, and may completely wash away some islets. Damage to human structures and crops may be complete.

As yet, there seem to be no discussions of "El Niño" effects specifically on the Marshall Islands, but it seems likely that the occasional droughts, especially in the northern atolls, may be results of this phenomenon. Exceptionally high rainfall does not result this far west. Typhoons may be generated farther east during El Niño years because of increasibg sea surface temperatures in the equatorial eastern Pacific.

SOILS

Taking as the definition of a soil "loose or soft materials on the earth's surface capable of supporting plant growth," atoll islets are mostly covered by soils. Even in bare platform surfaces there are crevices and sand-pockets where plants find a foothold. We can exclude the intertidal zone of beaches where the combination of movement and salinity seems to prevent establishment of plants. However, shallow mud and sand supports mangrove vegetation, rocky intertidal shores are covered by algae, reef-flats have a felt of green algae, and lagoon bottoms support sea-grass beds and certain algae, especially Caulerpa and expanses of Halimeda. No one seems to have treated these marine substrata as soils, excepting perhaps mangrove peat. They do cover substantial areas in the Marshalls, but have not been classified or described in soils terminology. Here we afford them only this brief recognition.

Terrestrial soils have had more attention (Stone 1951a, b, c; 1953a,b), (Fosberg 1954, 1957a,), (Fosberg, Arnow & MacNeil 1956), (Fosberg & Carroll 1965), (Hatheway 1952), (Sachet 1955). Modern specialized nomenclature has not been applied to the simple assortment of atoll soils and will not be attempted here. Several soil series have been described and named in the Marshalls, and will be briefly enumerated.

The simplest soil frequently found on Marshall Island coral islets apparently has no series name. It is almost pure white or pink coral sand, with no darkened A horizon nor any trace of a B deposition-horizon. This is, of

course, the youngest of all the atoll soils, deficient in most nutrient elements except calcium. It is found on beach-ridges and dunes.

The Shioya Series is of slightly altered coral sand and small gravel, with a somewhat darkened thin A horizon, with circum-neutral reaction. This is the most generally distributed and least differentiated soil series in the Marshalls, as well as in most other coral atolls and back-beach flats on high islands. It may be recognized by its generally light brownish-gray color, sandy texture and complete lack of coherence or structure.

The Arno Atoll Series is a comparatively well-developed soil with a friable usually fine-textured black A horizon, with a circum-neutral reaction, lacking a B horizon, and with light brownish-gray to buff colored C horizon not sharply set off from the coral sand or gravel, or consolidated platform parent limestone material. This series is found in the interior of larger moist to wet islets. The type locality is on Arno Atoll.

The Jemo Series is a rather localized, remarkable soil found only in association with *Pisonia* forest vegetation. It is characterized by a conspicuous A-0 horizon of pure mor-like raw humus with a definite acid reaction, variable in thickness to as much as 30 cm, no well-developed A-1 horizon but usually a transition to either a B or a C horizon, a notable but discontinuous B horizon which is either a crumbly highly phosphatic mixture of humus and coral sand or a hardpan of indurated "atoll phosphate rock," usually 5-20, rarely to 60 cm thickness, overlying a C horizon transitional to parent material of coral sand or gravel. The hardpan is found where there are or have been sea-bird rookeries and nesting colonies in *Pisonia* forest. It is formed by cementation of coral-sand particles by a brown calcium-phosphate precipitate, from acidified and dissolved phosphatic guano, washed down through the acid mor and neutralized by the coral sand. Subsequent leaching by percolation of acid solution of calcium phosphate gradually replaces the carbonate radicle in the lime sand particles by phosphate radicle, until in extreme old samples an almost pure calcium phosphate or hydroxyl-apatite remains. This process, at least in the Marshall Islands, only takes place under a pure or practically pure stand of the tree *Pisonia grandis*, which produces an acid raw humus which forms faster than it decomposes, thus accumulates to form an A-0, or humus horizon. In places where in pre-European time there were such stands of *Pisonia* forest, but which have been destroyed and replaced by coconut plantations, there often remain areas of truncated Jemo soils with the A-0 horizon missing and the phosphatic hardpan, in a weathered

condition, exposed on the surface. Known occurrences of Jemo soils, outside the Marshalls, are found even as far away as the Seychelles, in the Western Indian Ocean.

In the dry northern islands, such as Rongerik and Ailinginae, there apparently exists another soil series, unnamed and not yet described in print. This has never been studied and is only known from one or two poor manuscript profile descriptions and field observations on soil pits dug for other reasons. It has a brown granular A horizon. Its description and localization awaits investigation of these poorly known uninhabited northern atolls. It seems to be associated with a scrubby poor mixed forest, perhaps semi-deciduous in extreme dry seasons. Perhaps it may be a very attenuated Arno Atoll Series variant.

In all of the above-described soils, test pits frequently show "buried profiles" or at least buried traces of A horizons, sometimes even more than one in the same pit. A relatively recent example of such burial, exposed in a pit dug on Bikar Islet, suggests that these buried profiles result from storm waves or tsunamis sweeping vast amounts of coral-sand and debris over existing soils to such depth that a new soil development is initiated above the old buried one. The fact that huge coral-rock boulders are occasionally found well inland shows that waves carrying much suspended coral debris are not too unusual to account for known buried horizons.

Apparently no detailed soil mapping has been done in the Marshalls.

HYDROLOGY

Standing fresh-water is a rarity in the Marshall Islands. Running water is totally lacking except briefly during heavy rain-storms. Fresh ground-water does exist on most islets of any extent except in the very driest northern extremes of the archipelago. The ancient Marshallese, in all probability, knew of this and utilized it. Certainly they did in historic times, digging shallow wells, and making depressions down to the water table, close to mean tide-level, for taro cultivation.

In recorded geographical literature Charles Darwin, in an usually unnoticed passage in his Journal of Researches (new ed. pp. 452-453), was probably the first person to note the existence of fresh-water lenses of ground-water on coral atoll islets. Nothing much further was said about this phenomenon until the later 1940's (Fosberg 1948, 1949) and early 1950's (Cox 1951, 1953), (Cox, Davis & Wentworth 1951), (Fosberg, Arnow & MacNeil 1956) when extensive

investigations were carried out in various of the Marshall atolls.

It is now well-known that shallow Herzberg (or Ghyben-Herzberg) lenses of fresh-water float on the heavier sea-water in the porous interiors of atoll islets, except the very smallest and very driest. This diffuses out at beach level and is replenished by rainfall. This fresh-water is certainly responsible for the continued existence of deep-rooted plants such as trees on atolls. It can be reached by digging a few feet down into the interior of almost any atoll islet except those that have the soils underlain by platform rock. The water encountered is normally potable, though "hard" (limey).

VEGETATION

(See also Fosberg, F. R., 1953, Vegetation of Central Pacific atolls, a brief summary, A.R.B. 23.

The obvious present day vegetation of the Marshall Islands, as of most other coral atolls, is a forest of coconut palms (Cocos nucifera L.). This, of course, is a planted forest, and it has replaced most of the original natural vegetation of the islands. In addition to the area now occupied by the coconut plantations, the Marshallese brought other areas under cultivation. Pits for taro cultivation were dug down to below the fresh-water table in the interiors of the larger islets. Filled with muck, created from decomposing vegetable matter, they are planted to Colocasia and Cyrtosperma, the principal and most edible taro genera, as well as minor bits of sugar cane and a few marsh plants useful as food and medicines. Still other areas were cleared and occupied by villages and associated human sites. Western man has come and replaced or altered large areas of vegetation with his military, commercial and government installations. His war and weapons testing activities have altered entire atolls. Areas seriously altered, especially those now occupied or utilized by man are generally characterized by low biodiversity. This is because most of the native plants and animals have been eliminated, replaced by a relatively few planted or naturalized species, most of them not especially well adapted to the saline, highly calcareous atoll environment. Most are pioneer species, widely distributed weeds and "tropical tramps", or domesticated species dependent on the presence and protection of man. These, even though making up a significant part of the biota, and present in some cases in enormous numbers, are not the primary subject of this compilation, and in most cases will not be mentioned except as they may have a significant effect on the ecosystems described.

The object of the present effort is to indicate the nature and present location of such remnants of native ecosystems as may still exist. It is largely based on observations made 20 to 40 years back, hence some of what will be mentioned may now be gone. By describing them and indicating where they were and in what kinds of places, either the same examples may be relocated or similar other ones may be located. By revisiting and restudying some of these sites change may be documented and the dynamics of atoll ecosystems be better understood. Methods of protecting those set aside as natural areas may be better designed.

No record remains of the true original Marshall Islands vegetation. The Marshallese have been in the region for several thousands of years. Although they unquestionably altered the biota and environmental conditions, they probably had reached an equilibrium with the environment and most of the original species likely survived. Change has been more drastic since Europeans, Japanese and Americans have been in charge.

By studying what still remains we may mentally reconstruct something resembling the original ecosystems, except for components now extinct. By understanding and reestablishing favorable environmental conditions, we may rescue and redevelop some of the biodiversity with which the Marshallese lived in some measure of harmony.

Since vegetation is the most obvious and visible portion of most terrestrial, and some aquatic and marine, natural ecosystems, they will be characterized by their vegetation. And other components, when known, will be mentioned or discussed as appropriate.

The <u>Mixed Broadleaf Forest</u> is, as in most tropical areas, the most common and most obvious type of vegetation in undisturbed places in the Marshalls. On small tropical islands this is usually a low to medium stature forest with a closed canopy. In the Marshalls, as in other low coral atolls, it is composed of varying proportions of a small number of tree species, a few shrubs and a sparse to dense herb layer, again of a few species. Epiphytes are present in the wetter southern atolls, but there are very few species.

One of the principal situations in which the mixed broad-leaf forest survives is in the "wind-breaks." There are crescent shaped strips of forest on the windward sides of islets, especially those on windward parts of the reef, left more or less intact to protect the coconut plantations

and taro-pits from wind-blown salt spray. This cultural practice is a very beneficial one, both as a reservoir of natural diversity and in facilitating food and copra production in the difficult atoll environment.

Where the strip of vegetation left as a wind-break is fairly wide, the inner part may be reasonably typical broad-leaf forest of *Tournefortia argentea*, *Guettarda speciosa*, *Pisonia grandis*, *Pandanus tectorius*, *Allophylus timoriensis*, *Cordia subcordata*, *Hernandia sonora* and a few other less common species. *Lepturus repens*, *Thuarea involuta*, *Fimbristylis cymosa* and *Polypodium scolopendria* are common herb species. The outer fringes of these strips are mostly wind-sheared scrub of *Scaevola sericea*, *Suriana maritima*, and *Tournefortia*, sloping from the forest down to the top of the beach.

Birds are seen around these areas, especially reef-herons and occasional white terns and noddies. Birds are more common in inverse proportion to the closeness of human habitations and activities. Of course, the insects snails and other invertebrates associated with the plant species may survive here as well as their plant hosts.

The relative abundance of the tree species varies a great deal locally and in places single species may dominate or even form pure stands. Such forests which are completely dominated by one species are here treated as distinct vegetation types and described as such. Such mono-specific forest types, though common in temperate and colder climates, are not usual in the tropics. They are here probably a response to stressful environments and to the fewness of species in the atoll floras. In the case of forests of *Neisosperma oppositifolia*, the pure stands may be final stages in succession. The dense shade created by the *Neisosperma* and the ability of its seedlings to survive in its shade may give the species a crucial advantage, leading to its eventually succeeding the mixed forest in certain habitats.

Neisosperma forest was a fairly frequent type in the interiors of islets, at least in the somewhat moist northern atolls. It may also have existed in wetter southern atolls but has not been observed there by us. The trees are tall, with clear trunks up to several dm diameter, and have dense rounded crowns of large dark green leaves. The ground is commonly covered by a dense stand of seedlings of this species 1-2 dm tall, apparently in a state of arrested or at least slowed-down development. Here and there in such stands of these trees, we have observed spots where the canopy is thin and chlorotic. Here a few shrubs suoh as *Allophyllus timoriensis* may gain a foothold, but no reason

for these areas has come to our attention.

Pisonia grandis forest is another pure-stand type, formerly very common and wide-spread in the Marshalls and throughout the Indo-Pacific coral islands. The trees reach enormous size to 30 m tall and with trunks to 2 m diameter, and even larger; pale and smooth-barked, of very soft brittle wood. Very little or no undergrowth and practically no herbs exist here. The ground is covered by a brown spongy layer of "raw-humus" or "mor" of semi-decomposed leaf-litter, acid in reaction, as described above under soils, *Jemo Series*. This is indeed an uncommon phenomenon in lowland tropics and not found under *Pisonia grandis* in mixed forest, where the litter is not pure *Pisonia*. The shade here is almost as dense as in the *Neisosperma* forest. The *Pisonia*, though capable of reproducing from seed, does not produce a layer of seedlings in a *Pisonia* stand, but large fallen branches and trunks strike root where they touch ground, if sufficient moisture is available, and give rise to new young trees. This forest is favored as a roosting and nesting site by several tree-nesting sea-birds.

Although *Pisonia* forest may have been the most frequent and widespread forest type on Indo-Pacific atolls, ease in clearing and fertile soils made it the most susceptible to alteration to coconut plantation. Now it is one of the more rare types and in most parts of the Marshalls has disappeared, leaving behind traces in the nature of truncated Jemo soils, indicated by weathered bedded phosphate rock.

Tournefortia argentea dominates areas especially on narrow islets in the drier northern atolls. This species is one of the principal pioneers on new sand and gravel bars, denuded islets, and abandoned clearings. The trees reach a large size, and stands of it tend to be of only one generation, replaced by other species of trees and the vegetation changing to mixed broad-leaf forest. In climatically dry areas there are open stands of *Tournefortia* of scrub-forest stature, with an herb-layer of *Lepturus* and locally, *Sida fallax*, *Portulaca* spp. and *Fimbristylis cymosa*.

On hard limestone platform areas *Pemphis acidula* forms very dense pure forests of rather low stature. The trees are often close together, tangled and difficult to traverse. Fringes of this species line rocky shores along passes and other places where the sand and gravel may have been washed away.

Stands of *Suriana maritima* scrub line certain sandy shores, forming narrow strips of this one species,

resembling Pemphis in habit but greener in color and with more flexible, less rigid branches.

Sandy shores and berms are, however, much more likely to support stands of Scaevola sericea. Pure bright green-leafed tangled scrub of Scaevola 1-2 m tall, and much interlaced, are also found on narrow ends of islets and in places where storms may have destroyed former vegetation.

Other species that occasionally form small stands are Barringtonia asiatica, Cordia subcordata, and Dodonaea viscosa. These will be pointed out, where known, in the accounts of individual atolls.

Mangrove vegetation is not very extensive in the Marshall Islands, but does occur. Poorly developed and impoverished mangrove swamps are known on Jaluit, Arno, and Ailinglapalap atolls in the southern and wettest parts of the group. Northward mangroves, especially Bruguiera, are found mostly in inland low wet spots, termed "mangrove depressions." These are, at least in some cases, probably the result of planting of the propagules of Bruguiera by the Marshallese, who had uses for the trees. They form dense pure stands, but do not spread where there is no connection with the sea. Various scrub types occur, pure stands and mixtures of various shrub species and juveniles of tree species. Scaevola sericea is the most ubiquitous, followed by juvenile Tournefortia. Allophylus timoriensis is widespread but less common, as also Dodonae viscosa. Sida fallax dominates certain open drier areas, but is easily shaded out.

Most of the herbaceous species occur principally as herbaceous components of forest or scrub types, but several may form pure or mixed usually small stands in openings and in theinterior of dry northern islets. Lepturus repens is the only one to dominate sizeable areas, especially on Pokak Atoll. It is a bunch-grass that also produces loose tangles of wiry stolons or runners. It is one of the earliest pioneers on bare sand and gravel, and its seeds are carried by floating on water, wind, and birds.

Boerhavia, of several ill-distinguished species, is common on both open and shaded ground, and especially where birds are nesting. Similarily, Tribulus cistoides is most frequent in sea-bird colonies, its long runners, grayish leaves, bright yellow flowers and "puncture-vine" fruits are characteristic.

Tacca leontopetaloides, a tall herb with dissected leaves, fistulose stems and petioles, potato-like tubers, and leathery greenish flowers in umbels on top of long

peduncles, forms open stands here and there both in open sunny places and in coconut plantations.

Small patches of several Portulaca (purslane) species are common, especially in openings.

Fimbristylis cymosa is very common in open or crowded pure stands in pioneer situations, such as back-beaches, sand flats, and even in coconut plantations.

Sea-grasses are very rare in the Marshalls, only two stands of Thalassia hemorichii being known from shallow water in Ujelang and Ailinglapalap Atolls. Other stands probably exist, but have not been reported. This seems to be the eastern limit of Thalassia in the Pacific.

Several cryptogamic formations should be mentioned, three of them terrestrial and three marine, though many more marine algal communities might be defined if serious attention were directed to the problem.

The identifiable terrestrial formations are three.

(1.) An algal crust, of several Myxophyta, almost universally found on undisturbed loose coral sand, the sand grains, to a few mm depth, stuck together by the gelatinous sheaths of the algal cells and filaments. The crust is gray and friable when dry, soft and flexible greenish gray when wet. This may be a source of fixed nitrogen for the various pioneer ecosystems in which these crusts occur.

(2.) On pebbles, cobbles, boulders, and lithified limestone surfaces exposed to light is a layer of the limestone penetrated to up to 5 mm or more by endolithic, boring Myxophyta. These appear as a graying or blackening of the limestone surfaces (upper surfaces only, of pebbles, cobbles, and boulders), and a greenish zone on broken edges. This layer seems universal on these coral-limestone surfaces above high tide level.

(3.) On coral sand flats, and also on flat exposuras of lithified limestone, after rain or heavy dew, abundant colonies of Nostoc appear, abundant enough to cover the ground by large hollow pads or bubble-like dark brownish-green masses, gelatinous in nature, drying black when exposed to the sun. Nostoc is known to fix nitrogen, suggesting another nutrient source for pioneer ecosystems on atolls.

The algal ridge on the outer edge of windward exposures of fringing and barrier reefs is composed principally of stony species of Porolithon, smooth or rough, depending on the species. This is the actively growing, wave-resisting part of the reef, and contributes perhaps a preponderant part of the calcium carbonate of a windward reef.

The algal felt which covers the smooth almost imperceptibly sloping surface of the reef-flat on the windward side of windward islets, at or just below mean low-tide level, is a dominant stand of branching filamentous green algae of several genera, Microdictyon okamurae, Neomeris vanbosseae, Cladophoropsis zollingeri, and red algae of the genera Laurencia and Jania. Many other small algae are less common components of this wide-spread formation. This algal felt is the home of several abundant genera of foraminifera which are principal contributors to the pink sand so abundant in Marshall Island beaches.

Another recognizable, but poorly studied algal vegetation type is the "meadow" of Halimeda spp. on lagoon bottoms. The flake-like segments of this segmented calcareous green alga are the most abundant components of many, if not most, lagoon-bottom sediments, and of some fossil limestone facies.

Many other communities of marine algae remain to be studied and defined in recognizable terms (perhaps some have been in literature that I have not seen). A proper algal flora, or at least an annotated check-list of Marshall Islands algae is much desired. With such a basis, meaningful marine synecology could be arewarding enterprise.

LIST OF THE INDIGENOUS, POSSIBLY OR PROBABLY INDIGENOUS VASCULAR PLANTS KNOWN FROM THE MARSHALL ISLANDS, AND THOSE BELIVIED TO BE ABORIGINAL INTRODUCTIONS

Low coral islands, generally, have very small floras, compared with even moderately elevated islands. The reasons for this are a bit complicated and some of them are matters of some disagreement, as well as their relative importance. I will give, very briefly, my own views on this.

First, and most obvious, is that the plants must be able to tolorate considerable salinity, from salt spray and the occasional flooding by storm waves. This restricts the possible floras considerably. There is also the considerable likelihood that all low coral islands without any elevated limestone (feo in the Tuamotus), were completely submerged during the "post-glacial xerothermic period," when the world-wide sea-level was several meters higher than at present. If this is the case, the present floras are the results of colonizations within the last few thousands of years. The Marshall Islands have little or no elevated limestone of more than 1-2 meters. The third factor is isolation. Many atolls, including the Marshalls, are separated from continents and high islands, source areas of insular floras, by hundreds, often many hundreds, of

miles. Long-distance dispersal and successful establishment is, statistically, an infrequent occurrence. Low nutrient status (Fosberg and Carroll 1965) is another limiting factor. The soils of coral islands, derived from almost pure calcium carbonate, with some added guano, are generally very low in some of the minor nutrients, such as iron. Many plants do not thrive in such nutrient-poor situations.

One of the difficult problems in determining the number of native species is how to know that a species is or is not indigenous. Seldom do we have records of when a widespread species arrived. Many are obviously not native, but early collections show that some such have been in the Marshalls for a long time. In this compilation we have indicated the species as indigenous [I], of probably aboriginal introduction [A], and probably or possibly introduced by natural means, or doubtful [D]. Species marked [D] should be disregarded in estimating real natural diversity.

This compilation lists the species by the names that I consider correct. Some of these names may be unfamiliar, but to list all the synonyms would unduly extend the time the compilation required. Further information may be found in the three installments of our Geographical Checklist of Micronesian Plants (Fosberg, Sachet, and Oliver 1979, 1982 and 1987). The following additional symbols or abbreviations for habit and occurrence are indicated as appropriate:

Te - terrestrial
Ep - epiphytic
Aq - aquatic
Tr - tree
Sh - shrub
Vi - vine or creeper
Gr - grass
He - herb
Fe - fern
A - abundant
C - common or frequent
L - local
O - occasional
R - infrequent or rare

Application of some of these categories may be somewhat subjective, matters of judgement or opportunity for observation.

The genera are listed in the Dalle Torre & Harms sequence (slightly modified) familiar in most of American floras.

Psilotum nudum (L.) Beauv.
Eniwetak, Kwajalein, Majuro, Jaluit, Arno, Mejit.
(I] He, Tr, Fe, O-L

Ophioglossum pendulum L.
Namorik, Mili, Jaluit, Ebon.
[I] He, Ep, Fe, O-L

Asplenium nidus L.
Ailinginae, Kwajalein, Ailinglapalap, Majuro, Jaluit, Namu, Ebon.
[I] He, Te, Exp, Fe, L-A

Nephrolepis acutifolia (Desv.) Christ
Ailinglapalap, Majuro, Arno, Jaluit, Ebon, Namu.
[I] He, Ep, Fe, O-L

Nephrolepis biserrata (Sw.) Schott
Ebon.
[D] Fe

Nephrolepis hirsutula (Forst. f.) Presl
Kwajalein, Jaluit, Kili.
[D] He, Te, Fe, L

Polypodium scolopendria Burm. f.
Ailinginae, Taka, Utirik, Ujelang, Ujae, Wotho, Lae, Kwajalein, Ailuk, Likiep, Aur, Ailinglapalap, Majuro, Arno, Jaluit, Ebon, Eniwetak, Namorik, Wotje.
[I] He, Te, Fe, C

Pteris tripartita Sw.
Namorik, Jaluit, Ebon.
[I] He, Te, L

Thelypteris interrupta (Willd.) Iwatsuki
Arno, Jaluit, Ebon.
[I] He, Te, Fe, L-A

Vittaria incurvata Cav.
Namorik, Mili, Jaluit.
[I] He, Ep, Fe, L

Pandanus tectorius Parkinson (sens. lat.)
Bikar, Eniwetak, Bikini, Rongelap, Rongerik, Ailinginae, Taka, Utirik, Ujelang, Ujae, Wotho, Lae, Kwajalein, Ailuk, Jemo, Likiep, Aur, Majuro, Ailinglapalap, Namu, Arno, Kili, Jaluit, Ebon, Wotje, Mejit.
[I, A] Tr, Te, C
Edible varieties planted, propagated vegetatively.

Thalassia hemprichii (Ehrenf.) Aschers.

Ujelang, Ailinglapalap, Jaluit, Ebon.
[I] He, Aq, L-R

Centosteca [Centotheca] lappacea (L.) Desv.
Jaluit
[D] He, Te, Gr, R

Digitaria ciliaris (Retz.) Koel.
Rongelap, Kwajalein.
[D] He, Te, Gr, L

Digitaria radicosa (Presl) Miq.
Taka, Utirik, Kwajalein, Arno.
[I] He, Te, Gr, O

Digitaria setigera

Cyperus odoratus L.
Eniwetak, Lae, Jemo, Likiep, Ailuk, Kwajalein, Namu, Jaluit, Mejit, Wotje, Ailinglapalap, Ebon.

Digitaria setigera Roth
Eniwetak, Bikini, Ailinginae, Rongelap, Wotho, Lae, Utirik, Ujae, Kwajalein, Ailuk, Jemo, Likiep, Majuro, Arno, Jaluit.
[I] He, T, Gr, C

Lepturopetium marshallense Fosb. & Sachet
Eniwetak.
[I] He, Te, Gr, R
The only Marshallese endemic plant.

Lepturus gasparricensis Fosb.
Pokak.
[I] He, T, Gr, L-C
Endemic to Pokak and Wake Island.

Lepturus repens (Forst. f.) R. Br.
Pokak, Bikar, Eniwetak, Bikini, Ailinginae, Rongelap, Rongerik, Taka, Utirik, Ujelang, Ujae, Wotho, Lae, Kwajalein, Ailuk, Jemo, Likiep, Aur, Ailinglapalap, Majuro, Arno, Jaluit.
[I] He, Te, Gr, A
The commonest, most ubiquitous plant in the Marshalls.

Oplismenus hirtellus (L.) Beauv.
Majuro, Eniwetak.
[D] He

Oplismenus compositus (L.) Beauv.
Majuro, Arno, Jaluit, Ebon.
[D] He, Te, Gr, L

Growing in shade away from sea.

Setaria pallide-fusca (Schum.) Stapf. & Hubb.
Eniwetak
[D] He, Te, Gr, L-A

Stenotaphrum micranthum (Desv.) Hubb.
Ujelang, Arno, Jaluit.
[D] He, Te, Gr, L-A

Thuarea involuta (Forst. f.) R. Br. ex R. & S.
Eniwetak, Bikini, Ailinginae, Rongelap, Utirik, Ujelang, Ujae, Wotho, Lae, Kwajalein, Ailuk, Likiep, Aur, Ailinglapalap, Majuro, Arno, Jaluit, Namu, Wotje, Mejit, Ebon.
[I] He, Te, Gr, C

Zoysia matrella (L.) Merr.
Jaluit.
[D] He, Te, Gr, L

Cyperus javanicus Houtt.
Likiep, Majuro, Jaluit, Mejit, Ebon, Eniwetak, Namu.
[I] He, Te, L

Cyperus kyllingia Endl.
Arno, Jaluit.
[D] He, Te, L

Cyperus odoratus L.
Wotho, Lae, Kwajalein, Ailuk, Likiep, Ailinglapalap, Majuro, Arno, Jaluit, Namu.
[D] He, Te, L-C
Common in wet places.

Cyperus polystachyos Rottb.
Kwajalein, Majuro.
[D] He, Te, L

Eleocharis geniculatus (L.) R. & S.
Kwajalein, Ailuk, Likiep, Arno, Jaluit, Mejit, Ebon.
[I] He, Te, L-A
Locally abundant in wet places.

Fimbristylis cymosa R. Br.
Eniwetak, Bikini, Rongelap, Taka, Utirik, Ujelang, Ujae, Wotho, Lae, Kwajalein, Ailuk, Likiep, Mejit, Aur, Ailinglapalap, Majuro, Arno, Namorik, Jaluit, Ebon, Namu.
[I] He, Te, A

Cocos nucifera L.
Bikar, Eniwetak, Bikini, Rongelap, Rongerik, Taka,

Utirik, Ujelang, Ujae, Lae, Kwajalein, Jemo, Ailuk, Likiep, Wotje, Maloelap, Aur, Ailinglapalap, Majuro, Arno, Kili, Jaluit, Ebon, Ailinginae, Mejit, Erikub, Namu.
[A] Tr, Te, A
Principal economic plant.

Alocasia macrorrhiza (L.) G. Don
Ujelang, Kwajalein, Ailuk, Mejit, Majuro, Arno, Kili, Jaluit, Ebon, Namu.
[A] He, Te, O

Colocasia esculenta (L.) Schott
Lae, Likiep, Aur, Jabwot, Ailinglapalap, Majuro, Arno, Kili, Jaluit, Ebon.
[A] He, Te, L
Formerly a very important food plant, grown in muck-filled marshy pits or depressions.

Cyrtosperma chamissonis (Schott) Merr.
Wotho, Ailuk, Likiep, Majuro, Arno, Kili, Jaluit, Ailuk, Wotje Mejit.
[A] He, Te, L
Formerly an important food plant, grown in muck-filled marshy pits or depressions.

Cordyline fruticosa (L.) Chev.
Kwajalein, Likiep, Jaluit, Ebon.
[A] Sh, Te, L-C

Crinum bakeri K. Schum. (or Engler ?)
Rongelap, Utirik, Wotho, Likiep, Ailinglapalap, Majuro, Mili, Jaluit.
[A] He, Te, L
Cultivated, known only from the Marshalls but probably brought by the Marshallese, but possibly a cultivar of local origin from <u>Crinum asiaticum</u> L.

Tacca leontopetaloides (L.) O. Ktze.
Eniwetak, Bikini, Ailinginae, Rongelap, Rongerik, Utirik, Ujelang, Ujae, Wotho, Lae, Kwajalein, Ailuk, Jemo, Likiep, Aur, Ailinglapalap, Majuro, Arno, Kili, Jaluit, Namu.
[A] He, Te, C
Tubers used as food but not or rarely planted, spontaneous.

Dioscorea alata L.
Jaluit
[A ?] He, Vi, Te, L
Cultivated only?

Dioscorea bulbifera L.
Majuro

Musa sapientum L.
Ujae, lae, Kwajalein, Ailuk, Maloelap, Aur, Ailinglapalap, Majuro, Arno, Kili, Jaluit, Namu.
[A] He, Te, C
A series of sterile clones, planted for food, grown in sheltered places only.

Curcuma longa L.
Jaluit.
[A] He, Te, L-R

Casuarina equisetifolia L.
Kwajalein, Likiep, Jaluit
[A ?] Tr, Te, O

Peperomia gibbonsii C. DC.
Ailinglapalap
Same as P. ponapensis?

Peperomia ponapensis C. DC.
Lae, Ailinglapalap, Mili, Jaluit, Ebon.
[I] H, Te, L-O

Peperomia volkensii C. DC.
Ebon.
Same as P. ponapensis?

Ximenia americana L.
Eniwetak, Bikini, Ujae, Lae, Arno.
[I] Tr, Sh, Te, R

Artocarpus altilis (Park.) Fosb.
Eniwetak, Bikini, Rongelap, Utirik, Ujelang, Ujae, Wotho, Lae, Kwajalein, Ailuk, Jemo, Likiep, Mejit, Aur, Ailinglapalap, Maloelap, Majuro, Arno, Mili, Namorik, Kili, Jaluit, Ebon, Wotje.
[A] Tr, Te, C
An important food plant, many cultivars.

Artocarpus mariannensis Trec.
Eniwetak, Rongelap, Utirik, Ujae, Lae, Ailuk, Likiep, Arno, Jaluit, Ebon, Majuro, Namorik, Bikini, Mejit, Wotje, Ebon, Jemo.
[A] Tr, Te, C
Many hybrids with A. altilis.

Ficus microcarpa L.f.
Kwajalein (possibly introduced)
[D] Tr, Ep, Te, R

Ficus tinctoria Forst. f.
Ailinglapalap, Majuro, Jaluit.

[I] Tr, Te, O
On Majuro said to have been brought from the Gilbert Is.

Laportea interrupta (L.) Chew
Jaluit.
[D] He, Te, R

Laportea ruderalis (Forst. f.) Chew
Eniwetak, Bikini, Ailinginae, Rongelap, Taka, Utirik, Ujelang, Ujae, Lae, Ailuk, Jemo, Likiep, Wotje, Ailinglapalap, Majuro, Arno, Jaluit, Kili, Mejit, Jwajalein, Namu.
[I] He, Te, C

Pipturus argenteus (Forst.f.) Wedd.
Ujelang, Ujae, Lae, Kwajalein, Wotje, Mili, Ailinglapalap, Majuro, Arno, Jaluit, Namu, Ujelang.
[I] Tr, Sh, Te, C

Procris pedunculata (Forst.) Wedd.
Jaluit, Ebon
[I] He, Te, Ep, L-O

Achyranthes canescens R. Br.
Bikini, Rongelap, Taka, Uterik, Jemo
[I] He, Te, L

Boerhavia albiflora Fosb.
Eniwetak, Bikini, Rongelap, Rongerik
[I] He, Cr, Te, C

Boerhavia repens L. (s. 1.)
Bikar, Eniwetak, Bikini, Rongerik, Taka, Utirik, Ailuk, Likiep, Jaluit
[I] He, Vi, Te, O

Boerhavia tetrandra Forst. f.
Eniwetak, Bikini, Ailinginae, Rongelap, Rongerik, Taka, Utirik, Ujelang, Ujae, Wotho, Lae, Kwajalein, Jemo, Likiep, Mejit, Aur, Arno, Namorik, Jaluit, Ailuk, Majuro, Wotje
[I] He, Vi, Te, C

Pisonia grandis R. Br.
Pokak, Eniwetak, Bikini, Ailinginae, Rongelap, Rongerik, Taka, Utirik, Ujelang, Ujae, Wotho, Lae, Kwajalein, Ailuk, Jemo, Likiep, Ailinglapalap, Kili, Arno, Jaluit, Majuro, Namu, Wotje
[I] Tr, Te, C-L-A
Probably formerly dominant on many islands, now very locally so.

Sesuvium portulacastrum (L.) L.

Kwajalein
[D] He, Vi, L-O

Portulaca australis Endl.
Eniwetak, Bikini, Rongelap, Rongerik, Utirik, Ujelang, Kwajalein, Ailuk, Likiep, Majuro, Arno, Jaluit, Mejit, Wotho, Ebon, Wotje
[I] He, Te, O

Portulaca johnii v. Poelln.
Mejit, Wotje
Doubtfully distinct from P. lutea.

Portulaca lutea Sol. ex Forst. f.
Pokak, Bikar, Eniwetak, Bikini, Ailinginae, Rongelap, Utirik, Wotho, Likiep, Ailuk
[I] He, Te, L-C

Portulaca oleracea L.
Eniwetak, Bikini, Rongelap, Taka, Ujae, Kwajalein, Majuro, Arno, Jaluit, Wbtje
[D] He, Te, C

Cassytha filiformis L.
Eniwetak, Bikini, Ailinginae, Rongelap, Rongerik, Taka, Utirik, Mejit, Ujelang, Ujae, Wotho, Lae, Kwajalein, Ailuk, Jemo, Likiep, Aur, Ailinglapalap, Majuro, Arno, Jaluit, Namu, Wotje
[I] He, Vi, Ep, C-A
Parasite on many host plants.

Hernandia sonora L.
Bikini, Ujelang, Lae, Kwajalein, Likiep, Ailinglapalap, Majuro, Arno, Jaluit, Ebon, Namu, Wotho
[I] Tr, Te, L-C

Rorippa sarmentosa (Forst. f. ex D.C.) Macbride
Arno, Jaluit
[I] He, Te, L-O

Caesalpinia bonduc (L.) Roxb.
Ujae, Jaluit, Ailuk, Mejit, Wotje
[I] Vi, Te, L-R
All or mostly seedlings from drift seeds.

Caesalpinia major (Medic.) Dandy & Exell
Lae, Kwajalein, Arno
[I] Vi, Te, L-R
All or mostly seedlings from drift seeds.

Canavalia cathartica Thou.
Eniwetak, Rongelap, Ujelang, Ujae, Wotho, Lae,

Kwajalein, Jemo, Likiep, Ailinglapalap, Arno, Jaluit, Majuro
[I] Vi, Te, C

Canavalia rosea (Sw.) DC.
Majuro, Mejit, Ebon, Eniwetak
[I] Vi, Tr, R

Canavalia sericea A. Gray
Wotje, Ailinglapalap, Majuro, Arno
[I] Vi, Te, O

Entada phaseoloides (L.) Merr.
Jaluit, Eniwetak
[I] Vi, Te, R
Drift seeds, one germinated.

Erythrina variegata L.
Kwajalein, Likiep, Jaluit
[D] Tr, Te, O

Intsia bijuga (Colebr.) O. Ktze.
Ujae, Wotho, Lae, Kwajalein, Ailinglapalap, Majuro, Jaluit, Ebon
[I] Tr, Te, L-O

Mucuna urens Medic.
Ailuk, Ebon
Drift seeds that sometimes germinate but do not survive.

Sophora tomentosa L.
Bikini, Ujelang,.Ujae, Likiep, Kwajalein, Ailinglapalap, Majuro, Arno, Jaluit, Wotje, Ebon
[I] Sh, Te, O

Vigna marina (Burm.) Merr.
Ujelang, Ujae, Wotho, Lae, Kwajalein, Likiep, Aur, Ailinglapalap, Majuro, Ebon, Arno, Jaluit, Namu, Mejit, Wotje
[I] He, Vi, Te, C
Bears nitrogen-fixing nodules.

Tribulus cistoides L.
Eniwetak
[I] He, Vi, Te, L-R
Often found in terrestrial sea-bird rookeries elsewhere, rarely seen in Marshalls.

Suriana maritima L.
Eniwetak, Bikini, Ailinginae, Rongelap, Rongerik, Taka, Utirik, Ujelang, Ujae, Wotho, Lae, Kwajalein, Ailuk, Likiep, Aur, Ailinglapalap, Arno, Kili, Jaluit, Mejit, Wotje
[I] Sh, T, C-L-A

Often dominant in shore vegetation, especially on sandy shores.

Soulamea amara Lam.
Bikini, Rongerik, Utirik, Ujae, Wotho, Lae, Kwajalein, Ailuk, Ailinglapalap, Arno, Likiep, Wotje, Ebon
[I] Sh, Tr, Te, O

Euphorbia chamissonis (Kl. & Gke.) Boiss.
Eniwetak, Bikini, Utirik, Ujelang, Ujae, Wotho, Lae, Kwajalein, Ailuk, Likiep, Aur, Ailinglapalap, Arno, Majuro, Jaluit, Namu, Mejit, Wotje
[I] He, Te, C-L-A

Allophylus timoriensis (DC.) Bl.
Bikini, Ailinginae, Rongelap, Utirik, Ujelang, Ujae, Wotho, Lae, Kwajalein, Aur, Ailinglapalap, Majuro, Arno, Mili, Jaluit, Mejit, Wotje, Ebon, Likiep
[I] Sh, Te, C

Dodonaea viscosa L.
Bikini, Likiep, Wotje
[I] Sh, Te, L-C

Triumfetta procumbens Forst. f.
Bikar, Eniwetak, Bikini, Ailinginae, Rongelap, Rongerik, Taka, Utirik, Mejit, Ujelang, Ujae, Wotho, Lae, Kwajalein, Ailuk, Jemo, Likiep, Aur, Ailinglapalap, Majuro, Arno, Jaluit, Wotje, Ebon, Namu, Kili
[I] He, Vi, Te, C

Hibiscus tiliaceus L.
Bikini, Ujelang, Ujae, Lae, Kwajalein, Likiep, Aur, Ailinglapalap, Majuro, Namu, Arno, Jaluit, Mejit, Ebon, Kili, Eniwetak, Ailinglapalap
[D] Tr, Te, L-C

Sida fallax Walp.
Pokak, Eniwetak, Bikini, Rongelap, Rongerik, Taka, Ailuk, Likiep, Utirik, Ujelang, Ujae, Wotho, Lae, Mejit, Aur, Mili, Namorik, Majuro, Arno, Jaluit, Wotje, Mejit, Ebon
[I] Sh, Te, C

Thespesia populnea (L.) Sol. ex Correa
Kwajalein, Jaluit
[D] Tr, Te, L-O

Calophyllum inophyllum L.
Bikini, Rongelap, Rongerik, Utirik, Ujelang, Ujae, Wotho, Lae, Kwajalein, Ailuk, Jemo, Likiep, Aur, Ailinglapalap, Namu, Majuro, Arno, Jaluit, Mejit, Ebon
[I] Tr, Te, C

Mammea odorata (Raf.) Kosterm.
Arno
[D] Tr, Te, R

Pemphis acidula Forst.
Eniwetak, Bikini, Rongelap, Taka, Utirik, Ujelang, Ujae, Wotho, Lae, Kwajalein, Ailuk, Likiep, Wotje, Ailinglapalap, Majuro, Arno, Kili, Jaluit, Namu, Mejit, Ebon.
[I] Sh, Tr, Te, C-L-O

Barringtonia asiatica (L.) Kurz
Lae, Kwajalein, Likiep, Ailinglapalap, Arno, Jaluit, Namu, Mejit, Ebon
[I] Tr, Te, O

Rhizophora mucronata var. stylosa (Griff.) Schimper
Ailinglapalap, Ebon, Arno
[I] Tr, Aq, L
Found in mangrove swamp.

Bruguiera gymnorhiza (L.) Lam.
Bikini, Rongelap, Utirik, Lae, Ailuk, Likiep, Aur, Ailinglapalap, Aur, Ailinglapalap, Majuro, Arno, Jaluit, Ebon, Namu, Kwajalein, Wotje
[I] Tr, Aq, L
Found in mangrove swamps and depressions, distribution extended by planting by Marshallese.

Sonneratia alba J. E. Sm.
Ailinglapalap, Arno, Jaluit, Lib, Wotje
[I] Tr, Aq, L
Found in mangrove swamps.

Lumnitzera littorea (Jack) Voigt
Ailinglapalap, Arno, Jaluit
[I] Tr, Aq, L
Found in mangrove swamps and depressions.

Terminalia samoensis Rech.
Eniwetak, Bikini, Ailinginae, Rongelap, Rongerik, Taka, Utirik, Ujelang, Ujae, Wotho, Lae, Kwajalein, Ailuk, Jemo, Likiep, Majuro, Arno, Ailinglapalap, Jaluit, Ebon, Mejit, Wotje, Kili
[I] Tr, Sh, Te, C

Ludwigia hyssopifolia (G. Don) Exell
Likiep
[D] He, Te, L-R
Found in wet places.

Ludwigia octovalvis (Jacq.) Raven
Likiep, Majuro, Arno, Jaluit, Kili
[D] He, Te, L
Found in wet places, taro pits, eto.

Centella asiatica (L.) Urb.
Utirik, Ujae, Kwajalein, Ailuk, Likiep, Aur, Ailinglapalap, Majuro, Arno, Jaluit, Mejit, Namu, Wotje
[D] He, Vi, Te, C

Neisosperma oppositifolia (Lam.) Fosb. & Sachet
Eniwetak, Bikini, Rongelap, Ujelang, Ujae, Wotho, Lae, Kwajalein, Ailuk, Likiep, Aur, Ailinglapalap, Arno, Jaluit, Wotje, Utirik, Majuro, Ebon
[I] Tr, Te, C-L-A
Locally pure-stand dominant, now less frequent.

Ipomoea littoralis Bl.
Ujelang, Lae, Ailinglapalap, Majuro, Arno, Jaluit
[D] He, Vi, Te, C

Ipomoea macrantha R. & S.
Pokak, Eniwetak, Bikini, Ailinginae, Rongelap, Rongerik, Utirik, Ujelang, Ujae, Wotho, Lae, Kwajalein, Ailuk, Jemo, Likiep, Mejit, Aur, Ailinglapalap, Majuro, Arno, Kili, Jaluit, Ebon, Wotje, Namu
[I] Vi, Te, C

Ipomoea pes-caprae var. brasiliensis (L.) v. Ooslstr.
Eniwetak, Lae, Kwajalein, Likiep, Majuro, Jaluit
[D] He, Vi, Te, L

Heliotropium anomalum H. & A.
Eniwetak
[I] D Sh, R

Cordia subcordata Lam.
Eniwetak, Bikini, Ailinginae, Rongelap, Rongerik, Utirik, Ujelang, Uaje, Mejit, Wotho, Lae, Kwajalein, Jemo, Likiep, Ailinglapalap, Arno, Majuro, Jaluit, Kili
[I] Tr, Te, C

Tournefortia argentea L. f.
Pokak, Bikar, Eniwetak, Bikini, Rongelap, Rongerik, Taka, Utirik, Ujelang, Ujae, Wotho, Lae, Kwajalein, Ailuk, Jemo, Likiep, Aur, Ailinglapalap, Majuro, Arno, Kili, Jaluit, Ebon, Namu, Wotje
[I] Tr, Sh, Te, C-L-A

Clerodendrum inerme (L.) Gaertner
Eniwetak, Bikini, Ailinginae, Rongelap, Utirik, Ujelang, Wotho, Lae, Kwajalein, Ailuk, Jemo, Likicp,

Ailinglapalap, Majuro, Arno, Jaluit, Mejit, Wotje, Ebon
[I] Sh, Te, C-O

Premna serratifolia L.
Utirik, Ujelang, Ujae, Wotho, Lae, Ailuk, Likiep, Ailinglapalap, Majuro, Arno, Jaluit, Mejit, Wotje, Kwajalein
[I] Tr, Tc, C

Vitex trifolia L.
Kwajalein
[D] Sh, Te, R

Ocimum sanctum L.
Utirik, Ujae, Lae, Ailuk, Ailinglapalap, Majuro, Arno, Jaluit, Aur, Mejit
[A] He, Te, O
Planted and naturalized.

Solanum nigrum L.
Kwajalein, Arno, Jaluit
[D] He, Te, L-O

Hemigraphis reptans (Forst.) T. Anders.
Kwajalein, Majuro, Arno, Jaluit, Ebon
[I] He, Te, O

Aidia cochinchinensis Lour
Arno, Jaluit
[I] Tr, Te, O

Hedyotis biflora (L.) Lam.
Likiep, Majuro, Arno, Ailinglapalap, Jaluit, Wotje, Mejit
[D] He, Te, O

Guettarda speciosa L.
Eniwetak, Bikini, Ailinginae, Rongelap, Rongerik, Taka, Utirik, Ujelang, Ujae, Wotho, Lae, Kwajalein, Ailuk, Jemo, Likiep, Mejit, Wotje, Aur, Ailinglapalap, Kili, Majuro, Arno, Jaluit, Ebon
[I] Tr, Te, C

Ixora casei Hance
Kwajalein, Likiep, Ailinglapalap, Majuro, Arno, Jaluit, Ebon
[A] Sh, Te, O
Probably intorudced as an ornamental and naturalized.

Morinda citrifolia L.
Eniwetak, Bikini, Ailinginae, Rongelap, Rongerik, Taka, Utirik, Ujelang, Ujae, Wotho, Lae, Kwajalein, Ailuk, Jemo, Likiep, Ailinglapalap, Majuro, Arno, Jaluit, Aur, Namu,

Wotje, Ebon, Kili
[I-A?] Tr, Sh, Te, C
Widely used for many purposes.

Scaevola sericea Vahl
Pokak, Bikar, Eniwetak, Bikini, Ailinginae, Rongelap, Rongerik, Taka, Utirik, Ujelang, Ujae, Wotho, Lae, Kwajalein, Ailuk, Jemo, Likiep, Wotje, Aur, Ailinglapalap, Majuro, Arno, Kili, Jaluit, Namu, Ebon
[I] Sh, Te, C-L-A
Dominant shore plant.

Adenostemma lanceolatum Miq.
Lae, Ailinglapalap, Majuro, Arno, Jaluit
[D] He, Te, O

Wollastonia biflora (L.) DC.
Eniwetak, Bikini, Ailinginae, Rongelap, Ujelang, Ujae, Wotho, Lae, Kwajalein, Ailuk, Likiep, Aur, Ailinglapalap, Majuro, Arno, Namorik, Jaluit.
[I] He, Sh, Vi, Te, C-L-A

LIST OF INTRODUCED AND PROBABLY OR LIKELY TO BE NATURALIZED SPECIES OF VASCULAR PLANTS.

This list includes such species as I consider, with reasonable certainty, to be of human, post-aboriginal, introduction and which are known or suspected to be naturalized, that is, spontaneously reproducing themselves, in the Marshall Islands. Islands where they have been collected or reliably observed are listed for each.

The genera are listed in the Dalla Torre & Harms sequence.

Cenchrus echinatus L.
Utirik, Jemo, Kwajalein, Likiep, Ujae, Eniwetak, Majuro.

Chloris inflata Link
Eniwetak, Kwajalein, Bikini

Chrysopogon aciculatus (Retz.) Trin.
Jaluit, Kwajalein

Cynodon dactylon (L.) Pers.
Eniwetak, Kwajalein, Majuro

Dactyloctenium aegyptium (L.) Willd.
Kwajalein, Eniwetak, Jaluit

Eniwetak

Eleusine indica (L.) Gaertn.
Eniwetak, Kwajalein, Majuro, Namu, Likiep, Utirik, Mejit, Kili, Jaluit, Lae, Ujelang, Wotho, Ujae, Jemo

Eragrostis amabilis (L.) W. & A.
Eniwetak, Rongelap, Rongerik, Utirik, Ujelang, Ujae, Wotho, Lae, Kwajalein, Ailuk, Jemo, Likiep, Aur, Ailinglapalap, Majuro, Arno, Jaluit

Eragrostis scabrifolia Swallen
Eniwetak

Paspalum conjugatum Berg.
Arno

Paspalum distichum L.
Likiep, Kwajalein, Ailuk, Arno

Paspalum setaceum var. ciliatifolium (Michx.) Vasey
Kwajalein, Jaluit

Setaria verticillata (L.) Beauv.
Majuro, Eniwetak

Cyperus compressus L.
Kwajalein, Eniwetak

Cyperus rotundus L.
Jaluit, Kwajalein, Majuro, Eniwetak

Commelina undulata R. Br.
Jaluit

Rhoeo spathacea (Sw.) Stearn
Likiep

Canna indica L.
Kwajalein, Arno, Jaluit

Peperomia pellucida (L.) HBK.
Jaluit

Pilea microphylla (L.) Liebm.
Kwajalein, Ailinglapalap, Jaluit, Ujelang

Coccoloba uvifera L.
Jaluit, Eniwetak

Mirabilis jalapa L.

Eniwetak, Utirik, Kwajalein, Ailuk, Likiep, Ailinglapalap, Majuro, Jaluit, Mejit, Wotho

Achyranthes aspera L.
Eniwetak

Amaranthus dubius Mart. ex Thell.
Eniwetak, Kwajalein, Majuro, Jaluit

Amaranthus spinosus L.
Kwajalein

Amaranthus viridis L.
Eniwetak, Kwajalein, Arno, Jaluit, Majuro

Gomphrena globosa L.
Ujae, Kwajalein, Ailinglapalap, Majuro, Arno, Jaluit, Likiep, Mejit, Ebon

Lobularia maritima (L.) Desv.
Kwajalein

Kalanchoe pinnata (Lam.) Pers.
Kwajalein, Likiep, Arno, Jaluit

Cassia occidentalis L.
Ujelang, Jaluit

Crotalaria incana L.
Kwajalein, Jaluit

Crotalaria longirostata H. & A.
Jaluit

Crotalaria pallida Ait.
Jaluit

Desmodium adscendens (Sw.) DC.
Eniwetak

Desmodium incanum DC.
Kwajalein

Dolichos lablab L.
Kwajalein

Leucaena leucocephala (Lam.) deWit
Utirik, Bikini, Kwajalein, Ailuk, Likiep, Jaluit, Eniwetak

Mimosa pudica L.
Kwajalein

Euphorbia cyathophora Murr.
Utirik, Bikini ?, Kwajalein, Ailuk, Likiep, Majuro, Arno, Jaluit, Wotje, Ebon

Euphorbia glomerifera (Millsp.) Wheeler
Kwajalein, Majuro, Jaluit

Euphorbia hirta L.
Eniwetak, Bikini, Utirik, Kwajalein, Jemo, Likiep, Jaluit, Wotje

Euphorbia maculata L.
Kwajalein

Euphorbia prostrata Ait.
Bikini, Ujae, Kwajalein, Jemo, Likiep, Ailinglapalap, Majuro, Arno, Jaluit

Euphorbia rubicunda Steud.
Bikini, Ujelang, Kwajalein, Jaluit, Likiep, Utirik, Wotje, Eniwetak

Phyllanthus amarus Schum.
Eniwetak, Bikini, Utirik, Ujelang, Ujae, Lae, Kwajalein, Jemo, Likiep, Ailinglapalap, Majuro, Arno, Jaluit

Ricinus communis L.
Eniwetak, Bikini, Ailinglapalap, Jaluit

Gossypium barbadense L. (or G. hirsutum L.)
Utirik, Kwajalein, Majuro, Arno, Jaluit, Likiep, Mejit

Malvastrum coromandelianum (L.) Garcke
Jaluit, Eniwetak ?

Sida acuta Burm. f.
Rongelap, Ujelang

Sida rhombifolia L.
Jaluit

Carica papaya L.
Bikini, Rongelap, Taka, Utirik, Ujelang, Ujae, Lae, Kwajalein, Ailuk, Jemo, Aur, Ailinglapalap, Majuro, Arno, Kili, Jaluit, Likiep, Namu, Mejit, Wotje, Ebon

Terminalia catappa L.
Kwajalein, Likiep, Arno, Jaluit

Polypremum procumbens L.
Eniwetak

Catharanthus roseus (L.) G. Don
Kwajalein, Ailuk, Likiep, Ailinglapalap, Arno, Jaluit, Majuro, Aur, Mejit, Eniwetak

Cerbera manghas L.
Jaluit

Asclepias curassavica L.
Bikini, Lae, Utirik, Ailuk, Ailinglapalap, Majuro, Arno, Jaluit, Namu, Mejit
Often cultivated, rarely established.

Ipomoea triloba L.
Kwajalein, Jaluit

Heliotropium procumbens var. depressum (Cham.) Fosb. & Sachet
Kwajalein, Majuro

Lantana camara L.
Ailinglapalap, Jaluit, Likiep

Lippia nodiflora (L.) Michx.
Eniwetak

Stachytarpheta indica (L.) Vahl
Jaluit

Stachytarpheta jamaicensis (L.) Vahl
Kwajalein, Majuro

Stachytarpheta urticaefolia Sims
Eniwetak

Plectranthus scutellarioides (L.) R. Br.
Kwajalein, Jaluit

Capsicum frutescens L.
Arno

Nicotiana tabacum L.
Jaluit

Physalis angulata L.
Eniwetak

Scoparia dulcis L.
Kwajalein

Plantago major L.
Kwajalein

Asystasia gangetica (L.) Anders.
Kwajalein

Blechum brownei Juss.
Jaluit

Pseuderanthemum carruthersii (Seem.) Guill.
Bikini, Rongelap, Utirik, Ujae, Wotho, Lae, Kwajalein, Ailuk, Ailinglapalap, Arno, Jaluit, Majuro.
Usually planted, but occasionally naturalized or persisting.

Dentella repens Forst.
Majuro, Jaluit, Kwajalein

Dentella serpyllifolia Wall. ex Airy Shaw
Kwajalein

Hedyoti corymbosa (L.) Lam.
Kwajalein, Jaluit

Hippobroma longiflora (L.) G. Don
Likiep, Arno, Jaluit

Ageratum conyzoides L.
Jaluit

Bidens alba (L.) DC.
Kwajalein

Bidens pilosa L.
Eniwetak

Conyza bonariensis (L.) Cronq.
Eniwetak, Bikini ?, Kwajalein

Conyza canadensis (L.) Cronq.
Kwajalein, Majuro

Coreopsis basalis (Dietr.) Blake
Jaluit

Eclipta alba (L.) Hassk.
Kwajalein, Majuro
Possibly not to be distinguished from E. prostrata (L.) L.

Eclipta prostrata (L.) L.
Kwajalein, Majuro

Emilia fosbergii Nicolson
Kwajalein, Majuro

Emilia sonchifolia (L.) DC.
Kwajalein

Pluchea X fosbergii Coop. & Gal.
Kwajalein
Spontaneous sterile hybrid between P. indica and P. symphytifolia

Pluchea indica (L.) Less.
Eniwetak, Kwajalein, Majuro

Pluchea symphytifolia (Mill.) Gillis
Eniwetak, Kwajalein, Majuro

Sonchus oleraceus L.
Kwajalein, Majuro, Arno

Spilanthes iabadicensis A. H. Moore
Jaluit

Synedrella nodiflora (L.) Gaertn.
Kwajalein, Majuro, Jaluit

Tridax procumbens L.
Kwajalein, Eniwetak

Vernonia cinerea (L.) Cass.
Eniwetak, Bikini, Kwajalein, Likiep, Ailinglapalap

Wedelia trilobata (L.) Hitchc.
Kwajalein, Eniwetak

Zinnia elegans Jacq.
Kwajalein, Jaluit

MARSHALL ISLAND BIRDS

Birds are the most conspicuous group of animals in the Marshall Islands fauna, and will certainly be a major object of attention during the Biodiversity Survey and of almost any scientific visit. Because of the enormous concentration of birds on Pokak Atoll, a special list of birds observed there in our visit in 1952 is included in our description of that atoll; the same for Bikar Atoll. A complete list of Marshallese birds is given here, copied from Atoll Research Bulletin 127 (Amerson 1969).. Notes on the birds of Wotho are also included in the account of that atoll, given here. A account of Marshall Island birds seen on the U.S. Geological Survey expedition in 1951-1952, was published as Atoll Research Bulletin 114 (Fosberg 1966).

AVIFAUNAL DISTRIBUTION

GENERAL

Seventy-nine species of birds have thus far been recorded from the 50 atolls which make up the Marshall and Gilbert Islands and from the ocean surrounding them. Of these 79 species, 37 are seabirds (Table 37) and 42 are land and fresh-water birds (Table 38).

Seventy bird species have been recorded from the Marshall Islands; 43 species have been recorded from the Gilberts. Thirty-five species are found in both island groups; 35 are known solely from the Marshalls; 9 are known solely from the Gilberts.

SEABIRDS

Thirty-one seabird species have been recorded from the Marshall Islands; 25 have been recorded from the Gilberts (Table 37). Nineteen seabird species are recorded from both island groups; 12 are known solely from the Marshalls; 6 are known solely from the Gilberts.

Seven seabird species are resident breeders on both island groups; in addition, three species that are resident breeders in the Marshall Islands are possible breeders in the Gilbert Islands. Seven others (including two in question) are resident breeders solely on the Marshall Islands, while only two (including one in question) are resident breeders solely on the Gilbert Islands.

The resident, including probable and possible, breeding seabirds in the Marshall and Gilbert Islands all regularly occur at sea within their respective areas. Some are more common than others, mainly due to species feeding habitat preference (also interaction of surface water zonation and abundance of food). The three major feeding habitat categories, for Marshall-Gilbert seabirds, are coastal (beaches, recfs, lagoons), offshore (near islands or atolls), and pelagic. Some species may overlap or their ranges may vary at different times during the year. Table 39 shows which Marshall-Gilbert breeding species generally occur in the three feeding habitats.

Seven seabird species are known to migrate annually through the Marshall-Gilbert area from breeding grounds elsewhere in the Pacific. These migrant species are usually entirely pelagic and pass through the area quickly. Occasionally, due to storms, injuries, or sickness, individuals may occur on the islands; these are then considered accidental to the island avifauna.

One seabird species is vagrant in the Marshall-Gilbert area. Such birds are so classified because they are away from their normal migration routes. If these stop on an island, they are also known as accidentals to the island avifauna.

Seabird occurrence in the Marshall and Gilbert Islands.

- none recorded.
* none recorded, but probably vagrant in the area.
# none recorded, but probably migrant in the area.
& none recorded, but probably a visitor in the area.
+ none recorded, but probably occurs.

	Marshall		Gilbert	
Species	Island	At Sea	Islands	At Sea
1) Black-footed Albatross		Visitor		
2) Laysan Albatross	Accidental	&		
3) Phoenix Petrel		Visitor		
4) Kermadec Petrel		Migrant		#
5) White-necked Petrel	Accidental	#		
6) Black-winged Petrel		#		Migrant
7) Bulwer's Petrel	Resident breeder ?	Uncommon		Visitor
8) Pale-footed Shearwater		Migrant		+
9) Wedge-tailed Shearwater	Resident breeder	Uncommon		
10) Sooty Shearwater	Accidental	Migrant		Migrant
11) Slender-billed Shearwater	Accidental	Migrant		Migrant
12) Christmas Shearwater	Resident breeder	Uncommon		Visitor
13) Little Shearwater	Accidental			
14) Audubon's Shearwater				Visitor
15) Leach's Storm Petrel		Migrant		Migrant
16) White-throated Storm Petrel			Resident breeder ?	+
17) Red-billed Tropicbird				Vagrant
18) Red-tailed Tropicbird	Resident breeder	Common	Resident breeder ?	Uncommon
19) White-tailed Tropicbird	Resident breeder	Uncommon		Visitor
20) Blue-faced Booby	Resident breeder	Uncommon	Visitor	Visitor

21)	Red-footed Booby	Resident breeder	Common	Resident breeder	+
22)	Brown Booby	Resident breeder	Uncommon	Resident breeder ?	Uncommon
23)	Great Frigatebird	Resident breeder	Uncommon	Resident breeder ?	Uncommon
24)	Lesser Frigatebird	Visitor	&	Resident breeder	
25)	Great Skua		#		Common Migrant
26)	Jaeger	Accidental			
27)	Common Tern	Accidental	*		

Seabird occurrence in the Marshall and Gilbert Islands.

	Species	Marshall Island	At Sea	Gilbert Islands	At Sea
28)	Arctic Tern	Accidental	*		
29)	Black-naped Tern	Resident breeder	Rare	Resident breeder	Rare
30)	Gray-backed Tern	Resident breeder ?	+	Visitor	Uncommon
31)	Sooty Tern	Resident breeder	Common	Resident breeder	Uncommon
32)	Brown-winged Tern	Accidental	*		
33)	Crested Tern	Resident breeder	Rare	Resident breeder	Rare
34)	Blue-gray Noddy	Resident breeder	Uncommon		
35)	Brown Noddy	Rasidcnt breeder	Common	Resident breeder	Common
36)	Black Noddy	Resident breeder	Common	Resident breeder	Common
37)	White Tern	Resident braeder	Common	Resident breeder	Common

Land and fresh-water bird occurrence in the Marshall and Gilbert Islands.

	Speoies	Marshall Islands	Gilbert Islands
1)	Reef Heron	Resident breeder	Resident breeder
2)	Snow Goose	Accidental	
3)	Mallard	Accidental	Accidental
4)	Common Teal	Accidental	
5)	Gadwall	Accidental	
6)	European Widgeon	Accidental	
7)	Pintail	Uncommon Migrant	

8) Northern Shoveler	Uncommon Migrant	Migrant
9) Canvasback	Accidental	
10) Tufted Duck	Accidental	
11) Muscovy Duck	Introduced breeder	
12) Duck sp.	Accidental	Accidental
13) Domestic Chicken	Introduced breeder	Introduced breeder
14) White-browed Rail	Accidental	
15) Golden Plover	Common Migrant	Common Migrant
16) Black-bellied Plover	Uncommon Migrant	
17) Semipalmated Plover	Uncommon Migrant	
18) Ring-necked Plover	Uncommon Migrant	
19) Mongolian Plover	Uncommon! Migrant	
20) Plover sp.	Accidental	
21) Whimbrel	Common Migrant	Common Migrant
22) Bristle-thighed Curlew	Common Migrant	Common Migrant
23) Bar-tailed Godwit	Common Migrant	Common Migrant
24) Greater Yellowlegs	Accidental	
25) Spotted Sandpiper	Accidental	
26) Polynesian Tattler	Uncommon Migrant	Uncommon Migrant
27) Wandering Tattler	Common Migrant	Common Migrant
28) Ruddy Turnstone	Common Migrant	Common Migrant
29) Japanese Snipe	Accidental	
30) Sanderling	Common Migrant	Uncommon Migrant
31) Pectoral Sandpiper	Uncommon Migrant	
32) Sharp-tailed Sandpiper	Common Migrant	Common Migrant
33) Buff-breastcd Sandpiper	Accidental	
34) Stilt sp.		Accidental
35) Ground Dove		Introduced breeder
36) Friendly Ground Dove		Introduced, breeder?
37) Crimson-crowned Fruit Dove	Extinct breeder	
38) Micronesian Pigeon	Resident breeder	Resident breeder ?
39) Parrot sp.	Probably introduced	
40) Long-tailed New Zealand Cuckoo	Common Migrant	Common Migrant
41) House Sparrow	Probably introduced, possible breeder	
42) Indian Myna	Introduced breeder	

At-sea feeding habitat classification of seabirds that breed in the Marshall and Gilbert Islands.

Species	Coastal	Offshore	Pelagi
Bulwer's Petrel		x	x
Wedge-tailed Shearwater		x	x
Christmas Shearwater		x	x
White-throated Storm Petrel		x	x
Red-tailed Tropicbird			x

White-tailed Tropicbird			x
Blue-faced Booby		x	x
Red-footed Booby		x	x
Brown Booby		x	
Great Frigatebird		x	x
Lesser Frigatebird		x	x
Black-naped Tern		x	
Gray-backed Tern		x	x
Sooty Tern		x	x
Crested Tern	x		
Blue-gray Noddy	x	x	
Brown Noddy		x	
Black Noddy	x	x	
White Tern	x	x	

Accounts of Individual Atolls and Islands of the Marshall Archipelago

This section will provide a usually brief summary of available information for each member of the Marshall Group, roughly in order north to south in the Radak and Ralik chains. In each account there is a paragraph on location and general geographical features, then it mentions, or usually briefly describes, where possible, areas of special interest from the viewpoints of natural diversity and remnants of unaltered, unoccupied or unexploited land. These accounts are limited by the ready availability of appropriate information and the personal knowledge of the compiler. For some islands there is practically nothing on record. These are pointed out as possible objectives of field study. We offer apologies for the limitations, and for possible omissions of important sources. With the practical limits on time, it has not been possible to go much farther than our own files and library. The references listed may give clues to other pertinent information.

POKAK ATOLL

Pokak (Pokaakku, or Taongi) Atoll, 140° 43' N, 168° 57' E, is the northern-most of the Marshalls, lying about 150 miles NNW of Bikar, next of the Radak Chain. It is the least disturbed atoll (exception possibly Bikar) of the Marshall Group, uninhabited by humans, and, from some viewpoints, one of the most interesting. Climatically it is the driest, though no rainfall measurements are known, and presents almost a semi-desert aspect. Because of its interest as an important natural area it will be described here in more detail than will be devoted to any of the other 28 atolls and islands. This is especially necessary as it

usuallynot be practical to visit it or Bikar, because of distance and landing difficulties. The enormous bird populations also give Pokak special interest as a possible preserved area. Pokak and Bikar were set aside by administrative decree as protected areas by the administrator of the Marshalls District in 1962, which status probably still remains. Hopefully this status will be recognized and sustained by the new Marshallese Government. The following information is mostly from observations made on a visit by C. G. Johnson, geologist, and F. R. Fosberg, from July 20 to 27, 1952. (Fosberg 1955 a & b, 1965).

The atoll is roughly crescent-shaped, about 11 miles by 5, oriented north - south, convex side to the east. A single narrow boat-passage, passable at slack water for small boats, empties the lagoon through the reef on the west side. Water, driven by the Northeast Trade Winds, pours in over the reef on the east and northeast sides, filling the lagoon to a constant high tide level. During ebb tide the water rushes out through this passage almost like a waterfall. The lagoon is shallow, probably not exceeding 30 m depth, and has many coral heads and patches, some reaching the surface. A massive algal ridge lines the outer edge of the windward reef, while the south and west reefs are coral-covered narrow flats where landings can be made at high tide in quiet weather. An interesting feature, perhaps unique to Pokak Atoll, is the presence on lagoon shores of the westernmost islets, on east facing lagoon reef-fronts, and on the windward edges of coral patches in the lagoon, of a tiny algal-rim, a miniature algal ridge 10 15 cm high probably a response to wind-generated turbulence in the lagoon.

Not much is known of the marine fauna and flora, but superficially they seem rather rich. Turbo lajonkairi seems to replace T. setosa as the common turban shell and provides the principal housing of the large red hermit-crab, Coenobita perlat.

Ten islets lie on the southern part of the eastern reef and on the part that curves westward. The rest of the reef lacks dry land and has not been well-studied. The largest islet is called Sibylla, about 2-1/2 miles long and up to 300 m wide. Kamome Islet, northeast of Sibylla, is also quite large. High boulder ridges and sand ridges are a feature of these islets that indicates a history of severe storms. Large boulders are also scattered inland, obviously carried by typhoon waves. The seaward sides of most of the islets have boulder and cobble ridges, sometimes 2 or even more concentrically parallel, their outer margins lining or somewhat back from the actual shore. Inland on the wider

islets are sand flats and rubble flats. Back from the lagoon shores are low sand and gravel ridges. On both seaward and lagoon sides are stretches of exposed rock platform, of coral conglomerate, its surface flat, about 1 m above mean high tide level, their outer edges sloping down, forming a rough erosion ramp, to the level of the reef flat, near mean low tide level. Outside of this on the inner edge of the leeward reef flat on Sibylla Islet are three low stacks, one of them with a huge boulder perched on top of it, with a visible crack or seam between the top of the stack and the boulder. The top of the stacks are about on a level with the upper surface of the ledge of reef conglomerate that protrudes from under the beach ridges opposite the stacks. Clearly these stacks and the ledge are parts of the same former reef surface, on which boulders were thrown by storm waves. This situation is similar to that described by MacNeil (1950) in Okinawa, and interpreted by him as evidence of a post-glacial higher than present sea-level. The northern two-thirds of the seaward shore of Sibylla is backed by an enormous boulder-ridge, up to practically 6 m high.

On Bokdik (or South) Islet, the last of the series to the southwest, is what seems to be evidence of a still higher, perhaps 4 m, former sea level. On both sides of the islet are beach-rock series, sloping in opposite directions, with between them a platform of reef-rock, above high tide level, forming the body of the islet. On this, running lengthwise north-east to south-west, are many huge boulder-like masses of limestone, apparently remnants of a surface about 2 m above that of the platform. The rock seems clearly to be continuous with the platform, no crack or suture separating the two at any of the places free from debris and available for observation. They seem, without doubt, to be erosion remnants of a former limestone surface almost 4 m above present mean low tide level, corresponding to the 11-1/2 foot notch seen in coastal limestone in various places in the world.

On the lagoon side of several of the islets a deep notch is cut in the low (1 m) cliff formed by the projecting platform, the overhanging edge broken off here and there.

The soils of Pokak are mostly very immature, in general belonging to the Shioya Series, characterized by very little humus accumulation. Large areas of fine sand show little development beyond the stage of unaltered coral sand. Since these sandy areas are inhabited by large numbers of shearwaters, burrowing beneath the surface, they may have some phosphate, from the excrement, though visible guano was only very local, under trees, and not characteristic of the fine sand. Most of the Shioya soils are mixtures of coarser

coral sand and gravel of various textures.

Other than exposures of bare limestone conglomerate, mostly around the peripheries of islets, the only extensive substratum beyond those mentioned above is surface covered by a rubble of loose broken coral, from pebble to boulder size, with no sand showing in the surface layer, at least. It is usually stained gray from presence of endolithic blue-green algae. This frequently has little or no vegetation.

Botanically, along with Bikar, it is the most impoverished of the Marshalls, each having only nine species of flowering plants. The following list comprises the entire vascular flora of Pokak as of 1952:

List of vascular plants.

Lepturus gasparricensis Fosb.
Lepturus repens (Forst. f.) R. Br.
Boerhavia repens L. (s. %.)
Pisonia grandis R. Br.
Portulaca lutea Sol.
Sida fallax Walp.
Ipomoea macrantha R. & S.
Tournefortia argentea L. f.
Scaevola sericea Vahl

The vegetation is comparatively simple, but interesting. The following generalized description is a somewhat edited version of one prepared in the field in July 1952, during a rather extreme dry period. The ground-water, sampled at the center of the widest place on Pokak Islet, and at two places on widest part of Sibylla, was at least half as saline as sea-water, the only such instance found in many pits in a number of others of the Northern Marshall Atolls, in all of which were found potable water, hard, but usually no more saline than the Honolulu city water supply.

There are, basically, six vegetation types on Pokak, each dominated by a single species. Various combinations of these occur, as well as different aspects with regard to height, density, luxuriance, etc.

The type that gives the atoll its character is a sparse low scrub forest of *Tournefortia*. This is from two to six m tall, with occasional trees that may be taller. It is rarely so dense as to greatly impede walking. It may be found in almost any substratum, but is usually not on sand or only in patches. Locally it has an understory of *Scaevola*. This in places closed so as to make progress difficult without a machete. Ordinarily, where there is no *Scaevola*, the spaces between the trees may be occupied by sparse *Lepturus*, *Portulaca*, *Sida* or *Boerhavia*, the latter more abundant on pure broken coral substratum (this likely

because of lack of competition, as it does very well in sand in some spots).

The other forest type is a pure Pisonia forest, represented only by several patches on Kamome Islet. This is not over 6-8 m tall at most. The trees not over 2.5-3 dm in diameter are set rather closely, with complete canopy, but this was sparse at when examined because of smallness and fewness of leaves. Doubtless it may be dense in a moister season. In the greater part of this, root sprouts are so thick as to effectively crowd out anything else, but locally there are patches of grass, Boerhavia, etc. Judging from the presence of Tournefortia logs inside this, it is probably increasing. Comparison of 1945 and 1951 photos shows that the Pisonia forest patches are gradually enlarging. Also that the relation of Sida to grassy areas in the open part is not a constant but a shifting one.

A prominent type is a scrub, 1-2 m tall, of Scaevola sericea, either pure or with scattered Tournefortia trees. This is commonly so dense as to impede walking through it. It is also of a characteristic bright green or yellow green color. It generally covers the ground completely. It is often on rock or broken coral, but by no means always. The low spreading branches, when covered by wind-blown sand, send out roots and form new plants. It rarely has any ground cover of other species.

The other woody type is a usually low, thin scrub of Sida fallax. This varies from 0.5 to 2 m tall, and from rather sparse to so dense as to be unpleasant to walk through, but offers no real obstacle because of the weak nature of the shrubs. This may be a practically pure stand, but more often has scattered Tournefortia trees. Often it is accompanied by Lepturus, Portulaca, or Boerhavia, or any combination of these.

This may grow on either gravel or sand, rarely on broken coral. An extensive aspect of it is on sandy stretches, usually on the lagoon sides of the broader islets, occupied by rookeries of shearwaters, with numerous burrows. Here the Sida is usually mixed with one or more of the herbaceous species.

This type grades imperceptably into a bunch-grass savanna with one or both species of Lepturus. In its more luxuriant aspects this is on sand and is also occupied by shearwater burrows. On thin gravel deposits on rock, or on recently available gravel habitats it is very sparse and composed usually of very small tufts of grass.

The limits between this and the remaining type, a pioneer community of Portulaca lutea, are hard to define.

In sandy places on the lagoon side, especially around reentrants, and on rubble or even pure broken coral, *Portulaca* may exist in pure stand. Everywhere it tends to grade into the *Lepturus* type. On rooky places, or even some sandy ones, it may have appreciable *Boerhavia*. It may, and frequently does, form a thin ground cover under *Sida* scrub and *Tournefortia* forest. It usually is sparse, under any circumstances, and does not completely cover the ground.

A prominent feature of the landscape is open broken coral, usually the tops of boulder ridges or boulder flats, commonly on the seaward side or on the north ends of islets, absolutely devoid of macroscopic vegetation. These are of a blue-gray color, due to the presence, in the surface of the limestone, of microscopic algae (*Chroococcus*?).

Also a prominent feature are exposures of old reef-rock, just above high tide level, on both seaward and, especially, lagoon sides. These, also, are colored blue-gray, darker than the boulder ridges, by microscopic algae.

The vegetation of the shallow edges of the lagoon is, so far as observed, sparse nodular lithothamnion (encrusting fragments of coral, shells, etc.) and patches of *Caulerpa*. In the passages, also, *Cauleroa*, *Lithothamnion*, and *Turbinaria* occur.

The leeward reef and detached small reef platforms inside it are covered with a luxuriant growth of various species of *Porolithon*. The surface of these reefs is at about constant high tide level. Around their edges is found an irregular rim of a few inches, resembling a miniature lithothamnion ridge. In holes in this platform two species of *Caulerpa* are abundant and several other green algae much less so. *Microdictyon* forms conspicuous tufts on the surface.

The windward reefs were not examined closely. A rather irregular algae ridge of *Porolithon* is evident.

Patches of reef just inside the windward reefs are reported (by C. G. Johnson) to be essentially similar to those inside the leeward reef.

An outstanding feature of all the land vegetation at the time of these observations was the appearance of extreme dryness. The *Tournefortia* had lost all but terminal tufts of very small leaves much less than half normal size. *Scaevola* had also lost its lower leaves, but still presented almost normal sized leaves but fewer of them. In most places, it was flowerless and fruitless. The *Sida* bushes were practically all partially dead, some completely

so. The Pisonia leaves were only a fraction of their normal size. Boerhavia was generally purplish in color and had mostly lost the leaves from all but the most distal parts of the branches. Ipomoea macrantha had died back to short scandent branches with short leafy side branches. A striking thing about this species here is its forming a short thick trunk, about a 3-4 dm high, with short living branches, surrounded by dead long radiating twining stems. Both species of Lepturus were mostly gray-brown tufts, with all culms and most leaves dead. Only the crowns and small sheltered leaves were still alive. Portulaca showed less effect of the dryness than any other plants but even this was obviously wilted at the tips, and in many areas, flowerless.

An interesting fact in this connection was that the effects of drought were less obvious in the most sandy areas, such as the lagoon side of Kamome Islet and the lagoon ridge of Pokak Islet.

The Tournefortia trees on most parts of the atoll were partly dead, or at least had dead branches. Judging from the guano deposits under the trees, the dead limbs were the habitual roosting-places of boobies and frigate birds. Whether the limbs were dead from this cause, or whether the birds chose the dead limbs to sit on was not obvious. Because of the prevalence of dead parts of trees the vegetation had a very bedraggled appearance. This, of course, was intensified by the general sparseness of foliage on the trees and other plants, and the gray-brown color of the dry tufts of grass.

The Sida, at this time, also presented a very unluxuriant appearance. Practically all of the plants were partly dead, and the general aspect of the Sida scrub was one of dead gray sticks.

Terrestrial animal life is most evident in the form of birds, but the Polynesian rat, Rattus exulans, is common at least on the larger islands. A lizard, Emoia sp. small in size, is common. The other obvious animals are principally large hermit crabs, mostly Coenobita perlata, the principal scavenger organism in the terrestrial ecosystem. Insects and other small terrestrial arthropods are common, but not very obvious. Collections made on the 1952 expedition have mostly not been reported on, so it is not possible to list them.

The bird fauna of Pokak is perhaps the most important feature of the atoll from the standpoint of preservation of natural diversity. The incredible abundance of seabirds and shorebirds there may be some indication of the conditions on

the other atolls, and of atolls in general, before the arrival of human immigrants. There now seems to be almost a negative correlation between the abundance of birds and of humans on atolls and atoll islets.

Following is a list of the birds seen on Pokak during a week in July, 1952; annotations concerning abundance, habitats and behavior, are given in a quotation in the General section of this report.

Diomedea nigripes (offshore only)
Puffinus pacificus
Phaethon lepturus
Pluvialis dominica
Arenaria interpres
Numenius tahitiensis
Heteroscelus incanum
Phaethon rubricauda
Sula sula
Sula dactylatra
Sula leucogaster
Sterna lunata
Sterna fuscata
Thalasseus bergii
Procelsterna cerulea
Fregata minor
Egretta sacra
Anous stolidus
Anous tenuirostris
Gygis alba

Pokak Atoll is by no means the most luxuriant of the group -- in many respects it may be the most impoverished. It exhibits less diversity, in terms of numbers of species (except of birds), but it is a relatively undisturbed, almost unaltered island ecosystem, a rare thing, indeed, in these times. It does show enough diversity to serve as an interpretive base-line for estimating change in relatively dry coral islands. It also may serve as a reservoir from which colonization, at least of birds, might take place if in the future more favorable conditions are established for rebuilding natural communities in other atolls in the drier northern part of the archipelago.

It is perhaps not too extravagant to suggest that it would be an appropriate "crown jewel" in a system of natural areas in the Marshall Islands, should such a system be developed. It should be helpful that both Pokak and Bikar were declared protected reserves in the early nineteen sixties by the then District Administrator, Mr. Maynard Neas, Trust Territory of the Pacific Islands. According to Mr. Jack Tobin, former Trust Territory anthopologist, (conversation 1964), prior to annexation by Europeans, Pokak, along with Bikar and Jemo, were regarded by the Marshallese as a bird (and turtle) reserve. Birds, their eggs, and turtles could be taken, after proper ceremonies, during the one visit made during the year.

BIKAR ATOLL

Bikar is the second most northern of the Marshall Group, 12° 15' N, 170° 07' E, its reef is oval in shape 6-7 miles long, about 4.5 miles wide. In August 1952 there were 3 islets and 2 small gravel bars, though Firth, et al. 1945, says there were 8 small islands. Evidence of a relatively recent typhoon is abundant on the atoll and such

a storm may have swept away some small islets. On the west side is a single boat-passage, forked, Y-shaped, with a patch reef just inside, as is frequent with narrow reef-passages.

The largest islet, Bikar, is oval-shaped, with projections north and south, the wider central portion with a high sand ridge along the west side and the greater part covered by *Pisonia* forest, surrounded by a narrow zone of *Tournefortia*.

Almeni Islet, smaller, also has *Pisonia* forest, but lower in stature and much wind-sheared, in its interior; Jaliklik Islet, also has *Pisonia*.

Jaboero Islet, a gravel bar, not more than half meter or so above high-tide level, has only *Portulaca lutea* vegetation, but has a large nesting colony of sooty terns.

The *Pisonia* forests, especially on Bikar Islet, have thick layers of raw-humus and phosphatic hardpan. One buried occurrence of phosphate is as much as half a meter thick. These *Pisonia* forests have in most areas a notable shrub-layer of *Pisonia* root sprouts. Some large trees have been uprooted by storms, prying up slabs of phosphate. Some of the holes thus created were being filled by *Pisonia* root sprouts, others not.

A small clump of coconut palms, planted at the north edge of the forest on Bikar Islet, by people from Likiep, persists, producing nuts, but these were very small and with bitter water in 1952. Larger shells were on the ground.

Only 9 species of flowering plants were found, list given below. The low vegetation on the rocky open areas is generally sparse.

Pandanus tectorius Park.
Lepturus repens (Forst. f.) R. Br.
Cocos nucifera L.
Boerhavia repens L. (s. l.)
Pisonia grandis R. Br.
Portulaca lutea Sol.
Triumfetta procumbens Forst. f.
Tournefortia argentea L. f.
Scaevola sericea Vahl

Birds are abundant, 18 species listed below. Annotations are given in the part on Marshallese birds in the General section of this report. Red-footed boobies and noddy terns nest abundantly in the Pisonia trees.

noddy terns nest abundantly in the Pisonia trees.

Phaethon lepturus	Pluvialis dominica	Sterna fuscata
Phaethon rubricauda	Arenaria interpres	Thalasseus bergii
Sula dactylatra	Numenius tahitiensis	Procelsterna coerulea
Sula leucogaster	Heteroscelus incanum	Anous stolidus
Sula sula	Sterna sumatrana	Anous tenuirostris
Fregata minor	Sterna lunata	Gygis alba

The outstanding feature of Bikar is the nesting of green turtles, Chelonia mydas, especially on Bikar Islet. During three nights of observation in August 1952 over 300 female turtles came ashore to lay their eggs. The entire coastal sandy part of the islet is churned up by the nest-building, excavation of holes, egg-laying, and covering and concealing the nest-sites.

The turtle-nesting, intact Pisonia forest, Jemo phosphate soils, and large bird populations make this atoll a primecandidate for preservation as a natural area. This also would preserve the ancient Marshallese custom mentioned above.

TAKA ATOLL

This small uninhabited atoll lies at 11° 07' N, 169° 46' E, about 4 miles southwest of Utirik. There are 8 islets on the reef, the largest being Taka Islet, about 1/2 mile long, and not very wide.

In 1951 the lagoonward part of Taka Islet was planted to coconuts, denser near the lagoon, sparse and mixed with native vegetation toward the center. The soil in the plantation is sandy, Shioya type. In the center was a small Pisonia grove, trees about 20 m tall, at that time, battered by a typhoon earlier in the year, rather open but choked by Pisonia root sprouts. The soil here is black. Scattered Pisonia occurs on most parts of the islet. The outer half of the islet is covered by mixed scrub of Guettarda, Pisonia, Tournefortia, some Suriana and Pemphis, and Scaevola is common.

Lojiron Islet is small, has a low but rather dense Pisonia grove in the center, with Jemo soil with raw humus. This is surrounded by an interrupted scrub of Scaevola, Terminalia, Guettarda and Tournefortia. In openings are stands of Achyranthes caneseans and of Sida fallax. Openings in and near the Pisonia grove are choked with Pisonia sprouts. Large areas were apparently swept clean by the typhoon and are beginning to revegetate.

Wotwerok Islet is partially wooded with a scrub or scrub forest of Tournefortia, Scaevola, and Pisonia, rather

battered by the typhoon. Only 4 coconut palms were seen. The opener parts of the islet are one vast sooty tern rookery, the ground being covered by nesting birds, their eggs laid on the bare gravel, so numerous that one had to be careful not to step on them. When scared up the birds filled the sky, with a deafening clamor.

Some other birds were seen, but the sooty terns dominated the islet.

Taka Atoll has a rather impoverished fauna and flora, but was relatively undisturbed in 1951. A study of its recovery from the typhoon would be rewarding. All or large parts of it could well be preserved to document revegetation and colonization processes over long periods of time.

UTIRIK ATOLL

Utirik (also called Wutrok) Atoll, the third southward of the Radak Chain, lies at 11o 14° N, 169° 51' E, about 60 miles SSW of Bikar. It and south reefs.

Utirik Islet is the largest, about 1-1/2 by 3/4 miles, and is the location of the village. In 1951 it was recovering from a severe typhoon earlier in the year. This islet is almost completely planted to coconuts. A number of long-abandoned taro pits are in the interior. The only reasonably unaltered parts are a long narrow spit extending from the southwest corner; with interesting small dunes and much beach-rock. This after 45 years, should show the results of a long period of recovery from denudation by the typhoon. The other area is on the east side, with thickets of *Cordia*, *Guettarda* and *Pisonia* tangled with *Ipomoea macrantha*, and farther east, *Lepturus* grassland and then broken coral rock with a dense scrub of *Scaevola sericea* with old battered trees of *Tournefortia*, *Cordia*, *Guettarda* and *Pisonia*.

Bigarak Islet is partly planted to coconuts, the southern part, with a small mangrove depression with *Bruguiera gymnorhiza*. The rest of the island is mostly broken coral rock with a mixed scrub of *Scaevola*, with occasional trees, 5 to 8 m tall, mostly *Pisonia*, but with some *Tournefortia* and *Guettarda*.

Eeluk Islet, next to the north, had a sparse planting of coconuts on the lagoon side, with *Pandanus* trees very common. The outer part, eastward, is covered by a mixed scrub of *Pisonia* and *Scaevola*, with an outer cobble ridge with *Suriana maritima* scrub.

The smaller islets, probably less disturbed, were not visited. Bird populations on the islets visited were not prominent. Probably the other islets may still have better faunas.

A short visit to Utirik in 1956 showed an increase in weed establishment, and an interesting phenomenon of coconut trees felled by the 1951 typhoon but not completely uprooted, prostrate on the ground, then making a right angle and growing erect.

Utirik would justify a visit by a field party, especially to study the smaller islets. This could conveniently be combined with visiting Taka.

LIKIEP ATOLL

Likiep is one of the more populated, hence more altered atolls in the northern part of the archipelago. It lies at 9° N, 169o 18' E. It is a large atoll, about 23 miles long and at most 9 miles wide, with 44 islets, practically all planted to coconuts. Even the tiny islet just inside the south passage, which except for the few palms, had, in 1951, some woods.

Not much information on areas in anything like natural condition is available. Of some interest is the strip of natural scrub and scrub forest along much of the seaward coast of the islets visited which serves as a wind break, protecting the coconut plantations from wind-blown salt spray. This is mainly typical mixed broad-leaf forest and scrub, with a fringe of Scaevola on its outer edge. The profile typically slopes from the edge of the plantation down to the top of the beach.

The eastern point of Likiep Islet is of particular interest. At 200-300 m from the point the coconut plantation is replaced by mixed forest, which attenuates eastward. This point has a most intricate pattern of series of beach rock, dipping in various directions. A study of these might provide information on the geomorphological history of this part of the islet, and of coral islet geoparphic dynamics generally.

JEMO ISLAND

This fragment of a former atoll (?) lies at 10° 06' N, 169° 30' E, about 27 miles SW of Ailuk. Its reef extends about 5 miles to the east. The island is oval in shape, about 3/4 mile long, oriented slightly west of north. Landing is only possible on SW beach in quiet weather (party

landed Dec. 10, 1951, with no difficulty). In 1951 there was a small house near the landing. At that time the terrestrial aspects of the island were studied rather carefully and it was described in detail, and specimens of all plants and invertebrates seen were collected. It was here that the Jemo series of phosphatic soils was described and an interpretation of its origin was worked out. It is said, also, that Jemo was, in pre-European times, considered a turtle sanctuary, only infrequent visits being permitted, with turtles and eggs being taken in limited numbers, under close supervision by priests (Tobin, conversation 1964).

Around almost the entire island beds of beach-rock dip seaward. Above this, on the west, north and much of the east sides is a high sand ridge, 4-5 m above high tide level. This is lacking on the S and SE exposures, where the beach is made up of rounded cobbles and pebbles. On the SW side, about 15 m inland are large boulders, including a slab of beach-rock fully 18 square meters and 3 dm or more thick, which must indicate a powerful typhoon, responsible also, perhaps, for the cobble beach.

On the sand ridge on the west side is a magnificent grove of Pisonia grandis 20 m or more tall, trunks up to 3.5 m diameter, with closed canopy, no undergrowth except Pisonia root sprouts, a thick raw-humus and phosphate hardpan layer on the ground beneath. At the south end, this forest becomes mixed with large Tournefortia trees, some of them almost as tall as the Pisonia. and with trunks to 0.5 or more m diameter.

Around the house, in a small clearing, in 1951 was a veritable weed patch, with a few cultivated trees and shrubs, and many exotics, some of which, especially Carica papaya, had begun to spread into the coconut plantation. Pandanus trees were occasional.

Inland from the Pisonia zone was a very luxuriant and healthy coconut plantation, on a level area of black soil with some phosphate fragments, extending about half-way across the island. Eastward from this the soil changed abruptly to fine sand, probably blown inward from the dune ridge. Here the coconut trees became sparse, and mostly dead or dying, some topless trunks still standing, others fallen. Around some of these were abundant coconut seedlings, and a few young trees, healthy enough. In this area, and becoming very dense, is a mat-like layer of Triumfetta procumbens with Boerhavia and Casaytba. eastward being invaded by Scaevola, and locally, Tournefortia.

Along the east side the sand ridge, and southward, the level terrace, somewhat lower than the coconut area, is a

dense tall scrub or scrub-forest, or even taller forest of Scaevola on the outer edges gradually changing to Pisonia inland to the edge of the decadent coconut plantation. This forest, where well-developed, is rather clear beneath, in areas of lower stature toward the beach, it is dense and tangled. Inland, the old coconut plantation is patchily being replaced by young coconuts.

A more detailed description of the island, with suggestions of the succession taking place, is available. If a field party were able to visit Jemo, it would be desirable to prepare a careful description of the present vegetation, to compare with that of 1951.

Birds were common, many red-footed boobies and common noddies nesting in the trees, white terns, also, other birds less common.

AILUK ATOLL

Ailuk Atoll, about 15 x 7 miles oriented north-south, lies at 10° 13' N, 169° 59' E, 41 miles SSE of Taka. It has a deep lagoon, and a continuous reef the length of the straight eastern side. On this reef are all but two of the many small islets, with the largest, Ailuk Islet, at the southern end. On Ailuk islet is the village, home of all or most of the inhabitants.

On the westernmost point is Akilwe (Aglue) Islet, differing notably from the others. The lagoon side is planted to coconuts, rather open with grass and scattered native trees. The north and southwest sides, from lagoon to about two-thirds of the way to the west point, are lined with a dense mixed scrub of stunted examples of Scaevola, Tournefortia. Pandanus, Terminalia, Neisosperma, Soulamea, which on the windward islets make up most of the predominant mixed forest. The western point, from about two-thirds the distance from the lagoon, is lined by an enormous boulder-cobble ridge, evidence of a terrific typhoon in the not too distant past. Huge boulders are scattered some distance inland from this. The ridges are partly bare, partly covered by mixed scrub-forest, extending well inland, to where it is replaced by open grassland, of Lepturus, Digitaria and Fimbristylis. with scattered patches of scrub and trees.

The many islets on the eastern side show the effects of almost continuous exposure to strong trade winds. The coconut trees, planted on all the suitable sandy lagoonward areas, are protected by broad zones of mixed forest. Some islets are too small or too rocky for coconuts to succeed. These are bare or covered by scrub, especially of Pemphis, bare rock exposures on many of the islets support patches of

dense scrub forest of _Pemphis acidula_.

The following generalized description, prepared in the field after at least brief visits to most of the islets in 1952, will give an idea of the pattern on these eastern islets. The constant wind-exposure seems to be the controlling ecological factor. Birds, of at least 13 species, are fairly common, but not really abundant. This is not surprising, considering the presence of a large human population on the atoll.

These islets vary in details of their vegetation, obviously because of size, shape, and substratum, but do conform as variations around a general pattern.

The portion toward the lagoon beach is planted to coconuts. This is surrounded by a crescent of mixed forest, very dense, often of _Pandanus_ on the inner edge and in the outer part of the coconut grove. _Guettarda_, _Pandanus_, _Tournefortia_ and _Scaevola_ make up the taller part, next to the _Pandanus_ and coconuts. This slopes seaward (and windward) becoming more and more a scrub, largely of _Scaevola_. The horns of this crescent extend along the passage beaches. There is usually a margin of _Suriana_ or _Pemphis_ or both here. The outermost convexity is usually a very sparse beaten-down scrub often of gnarled bushes of _Pemphis_ and _Suriana_, sometimes _Tournefortia_ and _Scaevola_. This extends onto the denuded part of the islet.

Practically all of the islets seem to have had their outer parts denuded of soil by a typhoon or typhoons. Some still show bared root systems clinging to cracks in rock. Crowns and crown sprouts of _Pemphis_, gnarled and beaten down, submerged in sea water at high tide, persist here with small tufts of _Fimbristylis_ between them.

Plants observed growing where bases are covered at high tide were:

Pemphis acidula	_Scaevola sericea_
Fimbristylis cymosa	_Tournefortia argentea_
Lepturus repens	_Guettarda speciosa_

The slope from true forest at edge of coconuts to scrub to the windward is very characteristic of these islets on the windward side.

The islets are characteristically separated by expanses of flat solution-pitted and exfoliated reef rock, of conglomeratic or brecciated nature, cut back in deep embayments from lagoon side, these often surrounded by low undercut cliffs, tops at about high tide level. Channels

from seaward reef flat run into these with a very swift current on rising and high tides. Much fine material is carried lagoonward in these. Many of the intervening flats are covered by irregular sharp boulders. Some of these may have been deposited here, but mainly they seem to be formed here by the sea dissolving away weaker beds and dissolving along bedding cracks until weakened sections of beds collapse and break into boulders and smaller fragments, which are gradually moved lagoonward by inflowing currents at high tide. In edges of the lagoon this debris, with that from outer reef flats, characteristically forms large deposits at inner ends of passages, bars across channel mouths, and debris trains extending inward from corners of islets. This undermining and breaking process seems to be one of the most important ways by which the rock between tides and above is being removed, at least where there is much agitation of water.

The explanation of the cutting away of the rock from the lagoon side in passages is not obvious.

The windward side of Ailuk seems to have been a continuous platform of reef-conglomerate and confused series of beach-rock, frequently but not always outlining the present islets but at various angles within these outlines. The series outlining the islets usually dip away from the islets toward the passages and lagoon.

This platform is being cut away by solution, abrasion, and under-cutting and collapse at present, except where protected by loose material and vegetation.

The leeward reef, on the other hand, seems to have its surface below low tide, with coral masses growing up to about mean low tide, and abundant scattered boulders of all sizes strewn over surface, exposed at low tide. Corals are abundant, varied, and beautiful here, algae not very important.

MEJIT ISLAND

This is a small island, lying 53 miles east of Ailuk, 10o 17° S, 170° 53' E, surrounded by a very broad reef. It lacks a lagoon, though there is a "shallow inlet" or pond. The island is said to be "well cultivated and wooded with coconut and breadfruit trees.* There was in 1935 a population of 424, certainly large for such a small island. We have little information of any kind, and none on possible undisturbed areas. The broad reef and the "inlet" might be of interest for aquatic diversity.

WOTJE ATOLL

Wotje (or Romanzov or Otdia) is a large atoll with about 56 islets on its reef. It is about 26 x 11 miles, oriented east-west, lying on 9° 28' N, 170° 15' E, with a large deep lagoon and several ship passages. It was the first of the Marshall atolls to be scientifically studied, visited in 1815-1818 and 1823-1826 by Kotzebue's two Expeditions with A. von Chamisso and F. Eschscholtz as naturalists. It is the atoll frequently mentioned as "Radack" in scientific literature, given as the locality for many cited collections by Chamisso and Eschscholtz.

EBON ATOLL

Ebon is the southernmost, 04° 38' N, 168° 43' E, and one of the wettest of the Marshalls. It is roughly circular and has about 22 islets, the larger ones on the southern half of the reef, where is also the only boat passage. Ebon Islet is over 5 miles long and at one end is also quite wide. Some collections have been made of its flora, almost none of the other organisms. Only three bird species were known from there in 1969. Nothing is on record as to the condition of the vegetation, or whether any undisturbed areas remain, but not much can be expected, as there is a large human population. Since it is about the most luxuriant, climatically, a visit would be worth-while.

KILI ISLAND

A small island lying at 05° 34' N, 169° 04' E, about 1 mile long, a third of a mile wide, land area about 1/3 square mile. It has no lagoon, only a brackish pond and a fresh-water marsh or depression. It is totally planted to coconuts and breadfruit, and is the present home of the Bikini people, exiled because of radioactive contamination from nuclear weapons testing on their home atoll of Bikini. The beaches are mostly cobble and boulder, with two stretches of sand. Densely inhabited, there is not likely any remaining native vegetation or native terrestrial animal life, and nothing of interest to a biodiversity field party.

NAMORIK ATOLL

This small trapezoidal-shaped atoll, lying at 05° 36' N, 168° 07' E, 3.75 x 3.50 miles, in the southern, wet belt of the group, is interesting in having the greater part of the reef occupied by two relatively wide islets, with relatively narrow reef-flats and over a square mile of land area. There is no passage into the lagoon, even for small boats.

Apparently no scientist has visited this atoll, and no useful information is available. This atoll might merit a visit to determine if any areas of native vegetation survive, and to collect specimens and information on current diversity status.

LAE ATOLL

This rather small atoll lying at 08° 56' N, 166° 14', E, is about 40 miles SW of Kwajelein, roughly triangular in shape, 5 x 3.5 miles, with 17 islets on the north and south reefs. The one shallow boat passage is on the west reef. Some of the islets are very close together and most of them are broad enough to hold an effective fresh-water lens. The rainfall is high enough to support a luxuriant vegetation and a diverse flora for a coral atoll. There is a relatively small human population.

Apparently a considerable proportion of the land area is too rooky to be suitable for coconut culture. At least, except for the two largest islets, Lae and Loj, only the lagoon ward half or third of each islet was planted to coconut trees when the atoll was studied in 1952. What would be, on other northern Marshall islets, a narrow crescent-shaped windbreak belt of broad-leaf scrub and scrub-forest, is on most of the islets on Lae a substantial area of forest reaching 20-25 m in height, and with a fair number of tree species and several forest types. The proportions of the common species in these forests vary greatly, locally. The common tree species are *Pisonia grandis*, *Intsia bijunga*, *Neisosperma oppositifolia*, *Allophylus timoriensis*, *Guettarda speciosa*, *Pandanus tectorius*, and *Tournefortia argentea*. The *Tournefortia* trees are all large old trees, suggesting, because this is a pioneer tree on bare substrata, that these forests are not older than the life-span of a *Tournefortia* tree.

One of the more interesting and unusual forest types here is a pure stand of *Neisosoerma oppositifolia*, which seems at least potentially a climax forest type. The ability of *Neisosperma* to reproduce in its own shade, and the shade of other trees, even of *Pisonia*, makes it likely that if it gains a foothold, over the long haul it will replace its competitors. *Pisonia grandis*, with its strong tendency to root-sprouting, seems similarly able to maintain dominance, but invasion of *Pisonia* forest by *Neisosperma* has been observed, but not vice versa.

A curious phenomenon observed in mature *Neisosperma* forests is an occasional very small area where the trees are chlorotic and in some such places the stand thin and somewhat open. Where open there may be large shrubs of

Allophylus timoriensis. These spots seem to be more than just temporary, as the same spots showed in 1952 on 10-year-old air photos. There is no obvious explanation for this phenomenon, and it would be very desirable to locate such spots and examine them carefully during the diversity field investigation.

The general pattern of the vegetation on the islets of the north reef at Lae may be described as follows:

Coconut groves are small in relation to sizes of islets, on or near inner side of islet, semi-circular with the straight side toward the lagoon, convex side reaching to the middle or less of the islet. Outside this is a crescent-shaped area of natural vegetation conforming to outline of island and that of convex side of coconut grove.

Undergrowth in coconut groves is of Wedelia, Ipomoea, Tacca, etc., ground cover of Lepturus, Fimbristylis, etc. State of undergrowth is dependent on how recently it has been cleared out. Burning of trash is commonly practiced.

The mixed forest which usually is just outside the coconut grove is largely of Pisonia and Intsia, with isolated Neisosperma trees or small groups, occasional Guettarda, Pandanus, and isolated large old Tournefortia trees, no young ones. This forest has sparse undergrowth, mainly of young trees of the same species, with Ipomoea and Canavalia vines, etc. On most of these islets are patches, large or small, of pure stands of Neisosperma, more or less even in age, with pure Neisosperma seedling stands beneath. Sometimes these forests extend practically to the beaches.

Seaward and passageward the mixed forest changes to a belt of scrub, widest toward the sea, there usually almost pure Scaevola, more mixed and more luxuriant along passage beaches.

The lithified conglomerate exposures may have small stands of Pemphis acidula scrub or scrub-forest.

Lae IsIet, the largeat one, site of the village, occupies the entire eastern point of the triangle, extending both east and northwest. It is largely planted to coconuts and breadfruit, but has an area of native vegetation occupying the easternmost point and another on the western extension. The latter is covered by a stand of Neisosperma along the west passage beach-ridge, and for a short distance east along the south side. Locally there is some admixture of Pandanus and Guettarda. The outer margins of this forest are lined with a dense scrub of Scaevola, Guettarda, Suriana with some Pemphis, and tangled with Ipomoea, Vigna, and

Canavalia.

In the center of the islet is an area of partly overgrown old taro pits, some still in use (in 1952), others with small trees growing in and around them, those in use more or less occupied by the not very useful Alocasia macrorrhiza.

East of this, the eastern peninsula for about one-third the distance to the lagoon shore, is not planted to coconuts or breadfruit, but is partly densely forested, partly open. The open areas were, in 1952, blanketed with a dense tangle of Wollastonia biflora to a depth of one meter or more. The soil here is a loose accumulation of small coral pebbles with a little dark soil well down between them.

Surrounding the open area is a broad zone of mixed forest, largely dominated by Guettarda speciosa, with Pandanus and Allophylus. Locally Pisonia forms pure colonies. This forest occurs on what seem to be a series of boulder and cobble ridges, the largest one around the east point. On the south side, on an enormous storm deposit of boulders, is a forest entirely made up of Barringtonia asiatica, mostly 3-10 dm trunk diameter, but some positively enormous, but the largest ones are usually hollow and partly decayed. The appearance of the boulder deposit suggests that the boulders may have been thrown up after the forest had attained nearly its present stature. The highest seaward edge of this ridge reaches at least 5 meters elevation. The forest is perhaps 20 m tall, and is tangled with lianas of Ipomoea macrantha with stems as much as 4 cm thick. Thc outer slope of the boulder ridge is covered by a strip of mixed forest. The whole east peninsula is fringed with Scaevola scrub.

Loj Islet, the westernmost, is almost entirely planted to coconuts, except the extreme points which have a fringe of Scaevola, and a depression in the center occupied by a pure stand of breadfruit. A mat of Vigna marina is the principal ground cover in the plantations.

Lae Atoll is one of the more luxuriant and least disturbed of the inhabited Marshalls. The trees have more epiphytic mosses, lichens, etc. than is usual on coral islands. It would seem to merit much time and attention by a field party.

AILINGINAE ATOLL

This is an elongate, narrowly rectangular atoll, lying at 11° 08' N, 166° 24' E, about 15 miles long, 4 miles wide, oriented N-S. There are 25 islets, and their arrangement

somewhat unusual in that they are almost all on the west and south reefs. The atoll is uninhabited, but several of the larger islets are planted to coconuts, and people, probably from Rongelap, are said to visit to make copra.

All too little is known of the natural history of Ailinginae, except for the birds, which were studied by a party from the Pacific Ocean Biological Survey Program in 1967, and the atoll was looked at casually, by Fosberg in February, 1956. On this latter brief visit a few plants were collected and notes made on the vegetation on Sifo Islet. Examination of oblique air photos, taken in 1955, shows that Knox Islet, Knobuen Islet, Ribinouri Islet, Mogiri Islet, Manchinikon Islet, and Sifo are densely wooded, with Enibuk Islet mostly planted to coconuts, some on Sifo, and Eniwetak Islet grassy with scattered trees.

An all too brief visit to Sifo Islet showed that the greater part is covered by a scrub forest, principally of Guettarda, Tournefortia, Scaevola, Pisonia, and Cordia, very little Pandanus. In openings there is a ground cover of Lepturus,Triumfetta, Boerhavia and Portulaca. Along the lagoon shore, and hooking around the ends of the islet, is a narrow zone of scrub, mostly Scaevola sericea, about 3 m tall, interlocked and dense. Locally there are some Guettarda and Suriana a few bushes of Terminalia samoensis.

On the seaward (west) side is a broad cobble-boulder flat, some of it open, some covered by a sparse mixed scrub. The east part of the seaward side, on the reef flat, somewhat separated from the shore, are two large series of beach-rock beds. West of this are large rocks. The lagoon shore is lined by beach-rock, being eroded.

Part of the interior of this islet is covered by a forest of Pisonia, up to 20 m tall and Cordia up to 10 m. Locally one or the other is more abundant. The Cordia, in addition to growing upward and forming a secondary canopy, sends out long twisted lower branches running over or near the ground, forming a tangle that is exhausting to penetrate and traverse. Ipomoea macrantha festoons the trees and in thin places is a thick tangle of Wollastonia biflora. In the interior of this is a pronounced ridge, to 3-4 m high, of sand and pebbles. The soil in this forest is a peculiar loose brown granular material, also noted on Rongerik, but in neither place was there time to study this carefully, or to describe a profile. It seems to be associated with Cordia and Pisonia. This, along with other features of Ailinginae, would justify much more careful study. The natural diversity is perhaps less than on most other atolls, but disturbance and alteration have been far less.

AILINGLAPALAP ATOLL

This is a large atoll, lying at 07° 23' N, 168° 46' E, in the southern portion of the Ralik Chain, roughly W of Majuro and N of Jaluit. It is triangular-crescent shape, convex to the east, about 27 miles by 19 miles, with many islets scattered on all sides, the larger ones mostly around curves and angles in the reef. There is a large resident human population and the larger islands are planted to coconuts. Little reliable information on vegetation is available except on Ailinglapalap and Bikajle (Bigatyelang) islets, which were studied briefly by Fosberg in 1946.

The two mentioned rather elongate islands on the south reef are mostly planted to coconuts, except on the rockiest shores, planted down to the top of the beach. A few bits of broad-leaf forest remained here and there in 1946, and several small rock bottomed mangrove depressions. One of these, on Ailinglapalap islet, part called Airik, was completely dominated by <u>Lumnitzera</u> <u>littorea</u>, with brilliant scarlet small flowers.

Other mangrove depressions have <u>Bruguiera</u> <u>gymnorhiza</u> with occasional <u>Intsia</u> <u>bijuga</u> and, rarely, <u>Lumnitzera</u>. The edges are lined with <u>Pemphis</u> <u>acidula</u>.

On Airik, and Ailinglapalap islet also, is one of the very few real mangrove swamps in the Marshalls. This has standing water in the central part, connected by a small channel with the lagoon at high tide. <u>Sonneratia</u> <u>alba</u> and <u>Rhizophora</u> <u>mucronata</u> var. <u>stylosa</u> are the principal trees, with occasional <u>Bruguiera</u> <u>gymnorhiza</u>. The bottom is a gray calcareous mud or marl. Epiphytic <u>Nephroleois</u> <u>acutifolia</u> occurs on some trees.

The flora, in general, is rich for a coral atoll, reflecting the high rainfall. This mostly occurs as undergrowth in the plantations and fringes around rocky beaches, in small wooded patches, and in the mangrove areas. About 100 species were collected during parts of two days, April 25-26, 1946.

The principal areas of natural history interest are the mangroves. However, it is likely that some of the smaller islets may remain relatively undisturbed and worth investigating. The known bird fauna is meager, 4 species only. This may reflect the long-time presence of a large human population, or it may likely result also from the almost complete lack of investigation and observation.

On the lagoon floor, in rather shallow areas, were

observed some of the finest displays of tall branching corals seen anywhere in the Marshalls. These merit detailed observation and perhaps protection as a marine park or preserve. They could be observed very well, even by snorkeling.

NAMU ATOLL

This is a large elongate atoll, lying at 08° 00' N, 168° 10' E, 32 miles long, NW-SE, 2-7 miles wide, NE-SW, with a large number of islets, mostly scattered along the east reef and around the two ends, a single islet beside the northern of 3 boat passages on the west side. The islets are said to be mostly sandy, some places with considerable humus and some exposed rock. Rainfall is high, and the flora, as indicated by St. John (unpubl. data) is fairly rich for an atoll. There is a fairly large human population. Only 6 species of birds are recorded, but probably more are present in small numbers.

No information on vegetation is available except that most islets are planted to coconuts.

WOTHO ATOLL

This atoll, lying at 10° 06' N, 165° 59' E, shaped like a bent triangle, 19 by 9 miles, has 18 islets, mostly on the east reef and at the angles, several on the west reef where there is a wide but shallow pass. For its size it has considerable land area, and, though populated, probably retains intact more of the total Marshall Islands biodiversity than any of the other atolls and islands. It is moderately wet and hence, has many more species and more diverse ecosystems than do the less-disturbed atolls at the north end of the group. This is known from studies made by the U.S.G.S. Expedition in 1952, when much detailed reconnaissance information was recorded on vegetation types and patterns, and relations between vegetation and substratum. If much of this natural vegetation still survives after 35 years, Wotho will be one of the most important atolls for preservation of indigenous biodiversity in the Marshall Archipelago. The following descriptive remarks, though written in the present tense, portray the atoll as it was in 1952. Because of the fact that this atoll may well be the one receiving most attention in the Biodiversity Project, the vegetation and geographical information notes made in 1952 will be copied with little editing from the field notebook. These notes cover most of the islets in clockwise order around the atoll, starting with Wotho Islet, the largest, in the northwest corner of the atoll. There is much repetition, but these detailed notes may make possible comparisons that could tell us much

about the dynamics of Marshall Islands vegetation and even geomorphology.

The western part of this islet is partially separated from the larger part by a large bay on the seaward side, running up into a sandy reentrant that extends in almost to the lagoon. Along the entire lagoon coast of the islet is a broad low ridge of sand, several feet above the general level. The reentrant tapers out into a narrow shallow channel which becomes fainter lagoon-ward and disappears shortly before reaching the ridge along lagoon shore. The reentrant is bare in center, with a belt of sparse scrub along each side. This is composed of Suriana, Scaevola, Guettarda, etc. on deep pink sand.

The north beach of the smaller north section of Wotho Islet is a boulder beach, running up into a well developed boulder ridge, backed by a broad boulder flat at slightly lower altitude. This flat has sparse mixed scrub of Scaevola, Guettarda, Suriana, etc. with scattered trees of Tournefortia and especially Pandanus, extending some distance in, merging with scrub forest. The boulder flat, as it gets further from the ridge, especially on the east side has some sand between the boulders. There are openings with Lepturus and Cassytha in the scrub.

The reef here has a layer of coarse breccia, well consolidated, being stripped by solution along bedding planes or unconformities and subsequent wave action, from a previous solution surface (?) in finar grained rock, exposing old solution basins (?).

Boulder beach hooks around the point and runs part way down the passage beach to the main curve in it.

The west point of the island has a sparse grove of coconuts with Pisonia, Scaevola, Tournefortia, Soulamea, Guettarda, Pandanus scrub forest second story, undergrowth of young coconuts and tree seedlings, with openings with Lepturus, some Fimbristylis and Cassytha. Same thing further in but lacking coconuts. No ground cover except in thinner places where it is similar to that in openings but sparser, and occasionally under Soulamea trees, where seedlings form a carpet. Tournefortia very soon drops out, Soulamea becomes more abundant. Finally scrub forest is Soulamea and Scaevola.

Soil from sand ridge along lagoon almost to the center is a fine gray silty material, quite deep.

Near the center is a patch of Neisosoerma forest, almost a pure stand but with small admixture of Pandanus and

Premna. Neisosperma seedlings abundant. Here the soil is a coral rubbla, pieces rather small. Beyond this, again a fine gray soil, with same mixed scrub forest as on west point, with Intsia added. This changes close to the channel on the east, becomes sparser and lower, with more coconuts, then becomes a scrub of Scaevola, Suriana, some Terminalia and Tournefortia. Outer fringe of this mostly Suriana. Gravel flat beyond this is bare, with a few Suriana seedlings close to scrub, many Scaevola seedlings further out in channel.

Enerikau islet beyond narrow channel has a small dry coconut grove, open beneath, surrounded by sparse scrub forest of Tournefortia, Guettarda, Pandanus, and Scaevola. Very rubbley soil.

Along sandy reentrant back of scrub the belt is a mixed forest of Premna, Morinda, Soulamea, Pandanus, Neisosperma, Scaevola, etc. varying locally to pure Neisosperma, on fine gray soil.

This changes, following up the reentrant, to coconut plantation, at first with much undergrowth of Scaevola, Guettarda, young coconuts, etc. At head of reentrant plantation it becomes sparse, with little undergrowth and a ground cover of Lepturus and Fimbristylis with Cassytha and some Ipomoea macrantha, on fine gray soil.

Along the lagoon, back from the sand ridge, is a large open area with Lepturus, some Fimbristylis and Cassytha. being invaded by Wollastonia, Scaevola and Guettarda, a few young coconuts which are very yellow. Fine gray soil. Back of this and of houses in village is coconut plantation with a mat of Wollastonia. Back of this is tangled undergrowth of shrubs of Morinda, Pandanus, etc. tangled with Wollastonia, Canavalia, Ipomoea macrantha, etc. In the village the ground cover is Vigna, Lepturus, Thuarea, Eragrostis amabilis, Fimbristylis, Cassytha, Canavalia, Ipomoea, etc. Here are 4 large breadfruit trees.

Village consists of a long stone-lined path with houses at very wide intervals on both sides. Those on lagoon side are up on the sand ridge.

Back, along the sandy reentrant is a scrub belt, as on the other side.

On the southwest shore of bay is a belt of small sand dunes. On the exact south side is a sandy belt with scattered small boulders, many of them of Porolithon. The beach here is somewhat shingly. Along the southeast side are a few boulders and much sand back of the beach, further

in fine gray soil but much small rubble in it. In the more rubbly places, the soil is blacker. The undergrowth in the plantation is tall, and near the beach is mainly Scaevola.

The two sides of the bay are lined with beach-rock, the head has none. About half way out on southeast side the directions of the strike and dip become very confused.

The hook at the outer corner of the bay is lined with a boulder ridge and boulder flat back of it. On this is a mixed scrub forest of Pisonia, Guettarda, Neisosoerma, Tournefortia, Pandanus, Morinda etc. Tangled with Wollastonia and Ipomoea it gradually changes to Scaevola scrub as the point and outer beach are reached.

Seaward beach is sand, behind a well developed cuesta of beach-rock. There is a broad belt of Scaevola scrub sloping to seaward, gradually changing to Tournefortia inland, with much Guettarda. The beach is about 10 m broad, and Scaevola roots run completely across this to the beach-rock. There are boulders scattered inland through the scrub and into the forest for at least a kilometer.

The leaves of the Scaevola exposed to the constant wind and spray are thick and twisted and distorted, locally chlorotic.

Back of the scrub belt is a belt of forest 50-100 m wide. In from the boulder flat along the bay shore this is a mixture of Neisosperma, Allophylus, Pandanus, small coconuts, etc. The soil becomes less rocky and the rubble becomes smaller and is occasionally piled up into low rounded mounds of small broken coral. Further in rubble becomes less abundant and fine soil more so. The undergrowth in this forest is largely tree seedlings with some Morinda and Wollastonia, Ipomoea is common in the canopy and its thick rope-like gray stems are common beneath.

The forest gradually changes, away from the boulder flat to an open forest of Tournefortia, Guettarda and Pandanus. Here are occasional sand dunes (boulders scattered in tops of dunes) as much as 2 m tall. Inside this is an enormous area of almost pure Neisosperma forest, locally varied with tall Pandanus. The Neisosperma trees are about 40-50' tall, seldom 1' in diameter, mostly about 0.5' with tall straight clean trunks, branched only near top, canopy complete, no undergrowth. A carpet of seedlings 6-12' tall, ground completely covered with fruits. Soil fine gray, varying to fine rubble.

Locally there are spots, light on photos, where the

Neisosperma is yellow, even dying. There is no evident reason for this. Where there is any hole in the canopy, the seedlings are much taller than elsewhere. Boulders are sparsely and irregularly scattered throughout this Neisosperma forest.

The center of the island is a series of long winding troughs and ridges, most likely ancient taro pits. Much breadfruit here, some trees even in bottoms of pits. Mostly the pits are dense tangles of Clerodendrum, Vigna, Wollastonia, Canavalia, Ipomoea, young Pandanus, etc. Locally spots have been cleared out and Cyrtosperma planted. The bottom is deep wet muck in these places. Cyperus and Fimbristylis tend to choke out the Cyrtosperma.

The Neisosperma forest seems to represent a remnant of the original vegetation. Otherwise it is hard to account for the pure stand. The trees are not large, but there is little else. To have produced such a stand after clearing would necessitate a means of close sowing of the seeds and of eliminating all competing species. Over long periods they might well be eliminated but it would take at least the lifetime of the longest-lived.

On Wotho islet the grass, and, especially, the Fimbristylis, show strongly the effect of the drought, by being brown and partly dried up. Beach rock, dipping lagoonward, extends for some distance along south end of lagoon beach. It is pitted with rounded edges, probably abraded by wave-washed sand. Toward the south end, perhaps 200-300 m north of the point, there is an abrupt change in the height of the coconut trees, those to the south being lower. The south point has only mixed scrub and back from point mixed scrub forest.

The north third of Bokanaetok, a sand spit on the east reef, was examined. The spit is a long low ridge of sand on platform rock that is generally marked with several series of beach rock, that showing along lagoon beach mostly dipping toward lagoon, that on seaward mostly dipping seaward. However, one stretch of a single series of beds, lying between the seaward dipping beds and the main sand ridge dips lagoonward, making it look as though a stretch of the sand ridge has moved into the lagoon. The denuded outer flats are generally rather wide.

There is very little vegetation, only a few scattered Tournefortia and Scaevola bushes, on the thin sand locally found on these seaward flats. On the main sand ridge is a mixture of Scaevola, Tournefortia and Terminalia, varying in density from scattered to continuous, some Tournefortia trees 5-6 m high and 2-3 dm thick, but these are uncommon.

Where there are scattered bushes low mounds of sand have accumulated under them. Where there is continuous scrub the sand ridge is several feet higher, with highest line usually nearest the lagoon side.

On seaward side is one tiny patch of Suriana, and about one third the way from the north end is a large and conspicuous clump of Pemphis acidula, quite dense. On the lagoon side the leaves are rather thin, on the seaward side very thick. At 9-9:30 a.m. insects of various sorts were common on the west side of this clump while none were seen on the sunny side. The Pemphis was flowering.

The sand where there is no vegetation tends to be flat on top. It is fine, white to pinkish, and the surface may locally be held firm by an incipient algal crust. There is a loose layer of dead leaves under the bushes. Here and there are thin patehes of Lepturus in the bushy vegetation, none in open.

There is a small group of ragged coconut trees at north end, and very ragged individual trees here and there along the islet.

From the lagoon the vegetation all along seems to be scrub with frequent Tournefortia 2-3 times as general level of scrub.

North of this spit are some small patches of sand on the reef.

Then there is a small islet with two patches of vegetation connected by a rock flat. The vegetation of both halves is sparse scrub and there is one coconut tree on the south half. (Seen only from boat.) Between this and the end of Wotho Islet is a small bar on a rock platform. From a boat two bushes are visible on this.

Lojwa islet was seen only from the boat in the lagoon. On the lagoon side appear to be high beach rock beds, possibly undercut by lagoon waves, extending above all but most extreme high tides. Vegetation is a sparse scrub and scrub forest mostly of Tournefortia with some Scaevola, a few coconuts on lagoon side.

Iroijemau, Ujiej and Jibnao islets were seen only from the boat in the lagoon. These are all wooded, possibly mostly with Pisonia, as defoliation is very noticeable, but from appearance on aerial photos, rather mixed. The ends, and in case of Iroijemau, the seaward projection tapers off to scrub. On Iroijemau, MacNeil reports a single Pemphis

bush on the extreme end of the seaward projection, the rest of the scrub being _Tournefortia_ and _Scaevola_. This projection is bare rock. On each of these islets there is a small patch of coconuts on the lagoon side.

On the lagoon side of Iroijemau there is mixed forest of _Pisonia_, _Tournefortia_, and _Guettarda_. On this islet the lagoon beach is lined with beach rock with great slabs of it piled up on beach above. Some sand on the north end, this with scrub of _Tournefortia_ and _Scaevola_.

On Enejelto islet the entire lagoon beach, except for a few short stretches, is lined by lagoonward dipping beach-rock, and above this, great slabs of beach-rock are piled up to the top of the beach. The unusually strong lagoon waves are dissolving the beach-rock along bedding planes, cracks, etc.' the cracks apparently reauIt of undercutting along bedding planes. A slight ridge is developed here and there along lagoon beach, but it is not conspicuous. Along the entire lagoon beach, except for a short stretch of coconuts with _Scaevola_ between them, is a mixed forest of _Guettarda_, _Tournefortia_, _Pandanus_, _Pisonia_, _Neisosperma_ and _Scaevola_, tangled with _Wollastonia_ and _Ipomoea pes-caprae_. Here and there are small patches of _Lepturus_. Inward, _Pisonia_ becomes dominant, but is being replaced by a layer of young _Neisosperma_ trees.

In the center, at least of tha south end, is a solid forest of _Neisosperma_. In all of this forest sticks blackened by _Xylaria_ are common. Rats are common. The soil in the forest is fine and blackish, with varying admixture of fine rubble. Toward the seaward beach it becomes more sandy and has on the surface boulders strewn into the forest. Near the south end is mixed forest similar to that described for the lagoon beach, with, also, some _Canavalia_ tangled in it. This peters out into mixed scrub on the sandy extreme south end. The entire seaward beach is gravel, resting on flat reef conglomerate. Above it is a belt of _Tournefortia_ forest with a _Scaevola_ fringe.

Kabben Islet is a large triangular island with one lagoon coast and two seaward ones, an east and a southwest. There are also two passage beaches, one north, the other west, the latter not sharply marked off from the southwest seaward beach.

Most of the beaches are of sand or fine white gravel. Along the lagoon beach is a broad ridge of sand, broken into small dunes at the western end. The north passage beach is of pebbles, lying on beach-rock, changing to finer gravel seaward and around on seaward beach changing to sand. The pebble beach is backed by a low ridge of broken coral. The

south peninsula of the islet is surrounded by a pebble-cobble beach, high and steep, backed by a very broad ridge of boulders and rubble, 100-200 m wide. This beach rests on a pitted conglomerate platform, with remnants of a higher platform here and there not yet completely eroded away on the southwest side. The ridge and boulder beach extend around the point and to the beginning of the sparse scrub and the crescent of sand beach on the southwest side and a corresponding distance, perhaps 300 m or more, on the east side.

The southwest corner of the islet has a broad reef-rock platform, and three series of beach rock extend along the passage beach, dipping away from the islet, splaying out fan-wise toward the lagoon corner, but not reaching it. This part has a sand beach.

Along the top of the lagoon beach is a narrow belt or fringe of scrub of Scaevola with some Tournefortia, tangled with Wedelia. This is in the edge of the coconut plantation, on the sand ridge. The plantation, except immediately around an old hut, is choked with thickets. Near the lagoon these thickets are of Pandanus, Scaevola and Morinda, tangled with Wollastonia. Around the hut, where the thickets have been cleared, a thin tangled mat of Wollastonia covers the ground.

West of the center of the lagoon beach, Neisosperma becomes a component of the plantation thickets, with Guettarda and Pandanus; Neisosperma very locally forming almost pure stands, and with Neisosperma and Pandanus seedlings making up the undergrowth. From here westward the coconuts are very sparse, thickets dense. Back from the beach, in the region of the hut, Scaevola rapidly drops out. Guettarda, Morinda and Pandanus dominate the thickets and the whole becomes choked with young coconuts of all ages. Still further back the coconuts become sparse. There are large clumps of breadfruit, and Neisosperma becomes common.

Westward the plantation gradually changes to mixed scrub forest with a few coconuts. On the west end, behind the low dunes, there is open sand with a scattered scrub of Scaevola,Guettarda, Suriana and Tournefortia, with scattered trees of Pandanus and small coconut trees. On the sand is a well-developed algal crust.

On the north passage a belt of scrub, mostly Scaevola and very low on the seaward end, becoming mixed with Tournefortia and Guettarda, and taller toward the lagoon, occupies the ridge of broken coral. Back of this is a scrub forest of Tournefortia, Pandanus, Pisonia, Guettarda, Soulamea, with a little Scaevola and Terminalia. Locally

there is a ground cover of rather wilted Polypodium, and of Soulamea seedlings, these now mostly dead. A few saplings of the trees and a tangle of Wollastonia make up the undergrowth. In openings Lepturus and Triumfetta form the ground cover. The soil is small rubble, becoming finer inward.

Toward the edge of the plantation a few scattered coconuts, Cordia, Morinda and Allophylus are added to the scrub forest. The forest is generally not more than 10 m high, the canopy not dense, at least in the dry season. The undergrowth becomes thicker by addition of coconut seedlings. Wollastonia becomes more luxuriant. Conditions become slightly moister so that seedlings of Soulamea are able to survive. Probably this change to slightly moister conditions is due to lessened penetration of wind due to greater distance from the windward beach.

Inward from the east end of the lagoon beach, into sparse coconut plantation grown up to a scrub forest, Pisonia, Guettarda, clumps of Cordia, with Canavalia festooning everything. Inward a little way are several breadfruit trees, coconuts become scarcer. Locally Pisonia is dominant and makes very large trees. Under them is a well developed peat layer and no undergrowth. The soil of fine rubble soon becomes mixed with much dark gray-brown loam. This mixture is generally at least 3-4 dm deep, the rubble increasing downward. Soulamea becomes common, and further in, abundant. Guettarda is co-dominant with it, and Neisosperma appears, forming local patches. Inward these patches become more frequent and larger, until the large area of pure Neisosperma forest extending inward from the east coast is reached. The soil remains the same uneven mixture of loam and fine rubble. In the mixed forest around the pure Neisosoerma, Wollastonia behaves as a liana, straight stems going up into the canopy, then forming tangles.

Extending from the east coast in for some distance is a great roughly triangular area of pure Neisosperma forest. This has a layer of fruits on the ground and a continuous layer of seedlings, varying locally in height from 2 dm to 1 m. The height of the forest varies from perhaps 20 m sloping down to the east to perhaps 4-5 m. There it gives way to a narrow belt of scrub, mainly Scaevola, which lines the beach. There is some admixture of Guettarda, and locally clumps of Tournefortia trees. A characteristic of this scrub belt on the windward beach is the effect of strong grooves or channels in the surface of the vegetation, parallel to the wind direction, starting at the beach and becoming shallower and disappearing inward. This scrub belt extends the full length of the east coast, typically wedge shaped in cross section, thin edge at the top of the beach.

Along the inner sides of the Neisosperma forest great Pisonia trees are mixed with the Neisosperma. Here, also, are many patches where the Neisosperma is very chlorotic, and even some trees have died. Just inland from the Neisosperma forest is a mixed forest of great Pisonia trees, Neisosperma and a few old Tournefortia trees, a few Pandanus and small Allophylus. Undergrowth is of saplings of Neisosperma and a few of Allophylus. There are occasional scattered groups of the low rounded mounds of broken coral previously described. One old Tournefortia had fallen. Paced off it was about 45 m tall. A few of the Neisosperma here are old, but there is mainly a stratum of young ones about 10 m tall. The undergrowth is of young Neisosperma saplings and a few young Pandanus.

Northward near center of this part of the island is a sparse stand of coconuts choked with Guettarda, Neisosperma, Pandanus, etc. with seedlings of these and of coconuts making walking difficult. Then there is a section of scrub forest of Guettarda, Soulamea, Pisonia, and Pandanus. Between this and the east end of the lagoon beach is more choked coconut plantation.

The east coast scrub belt sends a narrow hook around the south point. This is backed by mixed forest, the transition being gradual Guettarda and Tournefortia replacing more and more of the Scaevola. Along the boulder beach of the southwest coast of the south peninsula, mixed forest comes right to the top of the beach. It is made up of Pisonia, Tournefortia, Guettarda and Cordia. Inland on the broad boulder flat Pisonia becomes dominant in this mixed forest, some of the trees being enormous. Inland from these is a large opening on the rubble flat filled with a deep mat of Wollastonia. In the inner edge of this is a grove of coconuts. The boulder and rubble flat along this coast is 100-200 m wide.

Along the central part of the southwest side is a wide sand flat with very sparse scrub, much open sand, Scaevola predominant. In the mixed forest on the rubble and boulder flat there is little undergrowth except occasional seedlings of the component trees, and inland, of Neisosperma which is rare as a large tree but is actively invading.

The Cordias, abundant near the beach, are enormous low spreading trees with immense gnarled trunks and great writhing horizontal branches just off the ground. Penetration is difficult.

Enearik Islet, the surface of which is all sand along the lagoon beach, is a broad dune ridge from 2 to 4 m above

high tide level. The seaward part is lower. On top of a high rounded dune on the south end are scattered large boulders, about 2.5-3 m above high tide. On this dune there is a grove of _Pisonia_, surrounded by _Tournefortia_ and _Terminalia_. Both the _Pisonia_ and the _Terminalia_ were practically leafless. North of this a large _Cordia_ forms a broad low tangled thicket. In the center are three patches of coconuts, the middle one back from the beach. Between them is a patch of _Neisosperma_. Here there are, for a short distance, two dune ridges, but they are lower than at the two ends. The west end and parts of the east and center are covered by a mixed forest of _Tournefortia_, _Pisonia_, _Terminalia_ and _Guettarda_. The edges of this and sparser spots are tangled with _Wollastonia_. Some of the _Terminalia_ has lost its leaves, some has not.

The lower ground back of the dune ridge is covered by uneven scrub forest, mainly _Tournefortia_, _Guettarda_ and _Pisonia_, of varying density. Toward the seaward beach, especially on the east and west ends, this thins out to a sparse scrub of _Scaevola_ with some _Tournefortia_ and some _Guettarda_. Much bare sand between the rounded bushes. A broad series of beach-rock, dipping seaward, lines the southeast beach, some beach-rock, also, on the south side, and along the southwest side. Drift seeds are unusually abundant on this island. The sand at about high tide level, and the beach sandstone beneath it, are curiously polished.

Ombelim Islet, a sand platform, somewhat uneven surface, 1.5-2 m, is covered by a single large grove of _Pisonia_, medium sized, perhaps 15 m tall, with undergrowth of root sprouts of _Pisonia_ about 1 m tall forming a definite layer. This is surrounded on all but the southwest side by a narrow belt of _Tournefortia_. The only other vascular plant is _Lepturus_, which forms a small patch on seaward side in the _Tournefortia_ belt, now dry. Peat layer is well developed in the central part only of the _Pisonia_ forest, from 2 to 8 cm thick, underlain by partially consolidated layer of sand 3-5 cm thick, this lying on loose sand. On top is a loose layer of dry leaves covered by guano stains.

Near center is a broad sand dune about 4 m above high tide. Some sand is piled up around the edges, burying the lower parts of _Tournefortia_ trunks. Waves cutting a low cliff in sand on north side, expose abundant _Tournefortia_ roots 4-5 m from the plants. Birds are abundant and the dead leaves, roots, branches, etc. are strongly stained by guano, but no noticeable accumulation of guano was seen.

Biken Islet is a sand platform with high beaches, general surface about 2 m above the high tide level, but uneven, one large dune hill being about 2 m above general

surface. Lagoon beach is being cut away by waves, leaving a 2 m sand cliff, with a pile of slabs of beach-rock at base, one slab up in center of islet on sand.

Vegetation is rather open *Pisonia* forest in center, some fair sized trees, some bare, several still with last season's leaves. Occasional thin patches of *Lepturus*, scattered *Boerhavia* and *Portulaca lutea*, latter nearly leafless, the thick stems carrying it over tthe dry season. a sparse belt of *Tournefortia* runs around the periphery, with a few *Scaevola* bushes. Many white-capped noddy nests in trees.

Mejurwon Islet - east passage beach, seen from east, very long. Outer third is boulder beach, middle third seems to be gravel, inner third sand. A well-developed belt of *Tournefortia* extends along entire beach, backed by coconut plantation. Lagoon beach is all sand. In the eastern part there is no very noticeable sand ridge. In the middle the sand ridge along the back of the beach is broad and low, but very definite, actually appearing to be two ridges. Westward, about the west third of it develops into conspicuous dunes from 6 to 10 feet high. Back of the lagoon beach is a broad belt of open scrub, of *Scaevola*, *Tournefortia*, *Guettarda*, occasional *Pandanus* and *Suriana*. Between them is open sand. On this are scattered pumice and scoria pebbles with network of roots on their under sides. Here and there in this belt are great clumps of *Calophyllum*. Their leaves are browned on tips or edges where much exposed to weather.

On the dunes to the west the scrub is about the same composition as on the sand flats back of the beach to the east, but with much more *Suriana*. In openings *Triumfetta* is often found, half smothered by sand. In other openings *Lepturus* is common and *Cassytha* is common parasite both on *Lepturus* and on bushes.

To the west, near point the scrub becomes taller and denser, and may be termed scrub forest.

The islet is extensively planted to coconuts, on a fine sandy gray-brown soil. The part of the plantation near the lagoon beach is rather well cleared out, with scattered small bushes, the ground covered by a mat of *Canavalia* or *Wollastonia*. Large *Calophyllum* trees are found around old house site and elsewhere where there might have been a house, just back from the beach scrub. *Calophyllum* is more abundant on this islet than anywhere I have been in the Marshalls. Probably this accounts for the abundance of *Calophyllum* drift seeds on the beaches of various islets of Wotho.)

Away from the lagoon the woody second story becomes more abundant, forming thickets, composed of Pandanus, Morinda, Terminalia, Soulamea, a little Cordia, tangled with Ipomoea macrantha and Canavalia, and choked with coconut seedlings of all ages. Walking is difficult. There is some ground cover of Polyoodium and Lepturus, the latter especially in small openings. In thin places in the plantation Tournefortia and Guettarda are very common, with Wollastonia on the ground.

Natives visiting this islet had gathered a bundle of dry Pandanus leaves and some copra and turtle eggs, as well as 3 or 4 dozen coconut crabs. Some of these had been roasted and the large claws tasted very good. A large individual from this batch was preserved in a tank of alcoholic specimens otherwise collected by MacNeil (unnumbered). The color varied on different individuals, dull purple usually predominating, but certain ones largely light blue.

Enebarbar Islet's east end is surrounded by pebble or boulder beach, lagoon beach west of this, sand. Seaward beach, as seen from west, is a high steep boulder ridge. Most of the islet is covered by dense Pisonia forest, reaching out to the seaward edge. Surrounded, on lagoon side, by a broken fringe of Tournefortia. A clump of coconuts at west end. Seen only from boat in lagoon.

Eneobnak Islet. A belt toward lagoon a sand flat, forming 2 parallel ridges, especially toward the west, where there are two more ridges, separated from the two lagoonward ones by an interval in which there is locally a little rubble. These ridges are generally sandy.

On the sand flat and two lagoonward ridges is a sparse stand of scrub of Scaevola, Guettarda and Tournefortia, much bare sand and much Cassytha on the bushes. Pumice is scattered commonly on this sand. Some of the pieces have patches of a root network on the bottom.

The rest of the islet is wooded with a mixed forest, in most parts rather sparse, made up of Tournefortia, Guettarda, Pisonia, Cordia, and Scaevola, the Tournefortia most abundant near the edges, the Pisonia almost dominant in center. Three sparse patches of coconuts are found near the lagoon side. They show evidence of the drought in having the recent clusters of nuts dwarfed or abortive, some nuts small on some of the older clusters. Trees in the westernmost clump mostly have no nuts. The forest is rather dense in center of widest part of island, where Pisonia is commonest, about 8-10 m tall, little undergrowth or ground

cover. To the west it thins out, becoming rather sparse, _Tournefortia_ more abundant, _Pisonia_ less, thin ground cover of _Lepturus_ with some _Boerhavia_, _Cassytha_ especially in open places. One can walk freely almost anywhere. More or less sand on east end near passage beach. Some _Terminalia_ here.

The low rounded mounds of small broken coral perhaps betray their origin here. A little to seaward of center of islet, where the soil is generally rather rubbly, low mounds of small pieces have piled up around root systems of _Pisonia_ trees, either surrounding them or on the seaward side. In a few cases the tree has fallen, leaving the mound, with the tipped up root system adjacent, lying toward the lagoon either contiguous or several feet away. There are examples in various states of preservation, one or two having sent up big sprouts from the fallen trunk, one having almost decayed away, and several lacking any root system, the mound alone surviving.

Around the peninsula that sticks out to seaward, from near the lagoon end of the east passage beach around to the concave bend in the west passage beach, is a well-developed boulder ridge, with _Scaevola-Tournefortia_ scrub on the northeast side, this changing inward to the forest described above.

Back of the west end are several channels between rubble or reef conglomerate flats. Water runs swiftly through these from seaward, where they are narrow. They are much wider toward the islet, then the current sweeps westward from each of them around the west horn of the islet.

Wotho birds - In general, birds are abundant on the smaller islets, relatively scarce on the larger ones. Nesting is mostly seen on the smaller islets. Terns, as usual, are the most abundant birds.

Frigate birds - A colony of well over a hundred roost on Ombelim Islet. During the hot part of the day they are mainly resting, toward evening they soar in numbers above this and other islets, or out over the sea. Several individuals are all black beneath. Some also seen over Biken Islet.

Terns - Both noddies, white terns, and rarely black-naped terns may be found fishing together, flying excitedly over schools of fish, diving for them, either in lagoon or out in open sea. After they are full the noddies rest in the water.

Brown booby - One seen several times around Biken

Islet. An immature one seen at sea west of Biken. One adult seen at Ombelim Islet.

Common noddy - Seen in small or moderate numbers over lagoon and at sea, a few on the larger islets. Many on Enejelto Islet. Many birds and several nests seen on Enearik I., with downy young. One bird scared up here that had difficulty flying because it had Pisonia fruits stuck over its feathers. Several nests on Biken Islet. Many birds seen on the long sand spit on the east reef. Some birds and one nest on Eneobnak, this low in a _Guettarda_ tree. Commonly seen, in middle of day, in groups on beaches.

White-capped noddy - Commonly seen fishing over lagoon or open sea, at any time of day. Some nests seen in _Neisosperma_ trees on Enejelto I., also about 20 nests on Eneairik. Hundreds of nests and a multitude of birds on Ombelim, in _Pisonia_ and also in _Tournefortia_, many seen holding a "conference" in _Tournefortia_ trees on seaward side. On the seaward side of Kabben Islet were a small group of nests in _Pisonia_ trees. Many nests in _Pisonia_ and _Tournefortia_ on Biken I.

White terns - To be seen generally almost anywhere, flying over lagoon or open sea in pairs or small groups, or fishing in flocks in company with other terns, or flying overhead on islets protesting intrusion into their privacy. Probably in most such cases there are eggs on the bare branches of the trees, but they are seen only with difficulty. Many terns seen on Ombelim Islet, where one egg was seen on a _Tournefortia_ branch, also one half feathered and one fully feathered young. On Enejelto many were flying overhead, protesting as though they had eggs in the trees. Many were flying over the long-sand spit on the east reef, also over Eneobnak Islet.

Black naped tern - Small flocks on various islets, invariably on or over sand projections or beaches on inner corners of islets. On Enearik there were 8 on the east corner and 4 on the west. On Ombelim there were 10 birds on the inner beach - the islet is too short for the corners to be distinguished. Six were seen fishing over the lagoon near Wotho at 6:30 p.m., and one with a flock of other terns near Mejurwon at about 4 p.m.

Crested tern - Rare here, possibly only one or two pairs. One seen at sea west of atoll. Two seen on Ombelim Islet.

Pacific Golden Plover - Seen in small numbers generally, on inner and outer beaches, and in interior

wherever conditions are at all open, on most islets. Often with turnstones, tattlers, or curlews.

Wandering tattler - Seen one or two at a time, usually on outer beaches or reef flats, or passage beaches, on most islets. Often in company of plovers or turnstones, or more rarely, curlews.

Turnstone - In small flocks of two to five on most islets, on beaches or reef flats. Often with plovers and tattlers.

Bristle-thighed curlew - Seen singly, in pairs, or as many as three or four on beaches and reef flats of most islets. Here often fairly tame, allowing one to approach to within 15 or 20 m before flying.

Whimbrel - Rare; one seen on Enearik Islet.

BIKINI ATOLL

Bikini, northernmost of the Ralik Chain, 11° 35' N, 165° 23' E, is familiar as the site of a series of nuclear bomb-tests during the 1940's and 1950's. Its vegetation was greatly altered and largely destroyed, especially by the hydrogen bomb-test in 1954. During current investigations of the possibility of decontamination of Bikini, with the aim of permitting the return of the Bikini people to their homeland, a study of the present vegetation was carried out, and a descriptive report prepared (A.R.B.).

No original vegetation remains, but the recovery has been notable. It is of interest in our context as an illustration of the processes of revegetation after extreme disturbance. In the report are suggestions for preservation of a number of the smaller islets for long-term observation.

ENIWETAK ATOLL

Eniwetak, at 11° 30' N, 162° 15' E, is familiar as one of the two Marshall Atolls used for testing of nuclear weapons in the 1940's and 1950's. It is a large roughly circular atoll with 43 islets mostly on the north, east, and south reefs. Its vegetation and terrestrial natural features were completely altered during and after the testing period. A research laboratory was maintained there for a number of years and much research was carried out, making it one of the better-known of the Marshall Atolls. For the purposes of the biodiversity survey it is only of interest for its marine features and for studies of the recovery of vegetation after devastation.

MILI ATOLL

This is one of the larger atolls of the group, lying at 06° 08' N, 171° 55' E, 23 miles long, 13 miles wide, roughly rectangular, with over a hundred islets, well-distributed on the reefs. It has a substantial human population. A large number (22) of bird species are known from Mili, some collected by Japanese collectors, others recorded by non-scientific visitors. Nothing is on record about the vegetation of Mili, and relatively few records of plant specimens from the atoll. I would expect that some of the small islets might be relatively undisturbed, and might be considered for protection as natural areas, but this is merely a probability. No actual information is available.

AUR ATOLL

Aur is a medium sized rather wet atoll lying at 08° 16' N, 171° E. It is diamond-shaped, 15 x 9 miles, oriented NW-SE. About 42 islets are mostly on the east and northeast reefs, the largest are at the angles in the reef. Quite a number of species are known from the atoll, but there seems to be no recorded information on its vegetation. The island has had a considerable human population for a long time, so it can be assumed that at least all of the favorable habitats are planted to coconuts.

KNOX ATOLL

This small atoll, lying at 05o 55' N, 172o 09' E, just SE of Mili Atoll, is elongate, 4 miles long, oriented NW-SE, with broad reefs, very small lagoon, and about 10 islets. Almost nothing is known of it, scientifically. The coconut is the only plant on record, and not a single plant specimen from there is known to me. Sparse to dense vegetation has been mentioned. There are no permanent human inhabitants. There is said to be a boat passage on the west side.

ARNO ATOLL

Arno, lying at 07° 05' N, 171° 41' E, is a large, 21 miles long, 6-15 miles wide, irregularly crescent shaped atoll, with many (said to be 133) islets well-distributed around its reef, several of them, Ine, Ijen, and Rakaru quite elongate, occupying much of the southern reef. It contains approximately 5 square miles of land surface. The site of the 1950-1952 Pacific Science Board study, Arno is certainly the best studied of the Marshall Group, though perhaps more time has been devoted to Bikini and Eniwetak. Outstanding among the published results of the PSB study is the treatment of the vegetation by Hatheway (1953). This

multifacetted treatment should be consulted by all the members of the Biodiversity Project team. Here will be given some generalizations from Hatheway's work.

Arno has had a long history of human occupation and had a population of 1000 in 1952. Hatheway concludes that most of the vegetation is either presently planted coconuts and breadfruit, or secondary, or seriously altered stands of mostly native plants. However, in addition to the predominant secondary broadleafed mixed scrub-forest, he describes several restricted types of vegetation in particular habitats that may be not seriously altered, or even like original vegetation.

Storm ridges (boulder ramparts) on the seaward coasts of windward islets are covered by a dense scrub of Scaevola sericea, with some admixture of Tournefortia argentea, Guettarda speciosa, Terminalia samoensis, Pandanus tectorius, and Pemphis acidula. This scrub is wind-sheared, sloping upward from the beach-top to the forest inland. Stony flats, inland from the scrub zone support a belt of native mixed broadleaf forest of 14 species of native trees, 5 to 20 m tall, the zone to 100 m wide. Tree species present were Pandanus tectorius, Neisosperma oppositifolia, Guettarda soeciosa, Tournefortia argentea, Cordia subcordata, Intsia bijuga, Allophylus timoriensis, Pisonia grandis, Hernandia sonora, Barringtonia asiatica, and, in smaller numbers, Terminalia samoensis, Scaevola sericea, Pipturus argenteus, and Soulamea amara. Herbs on the ground were Asplenum nidus, Polypodium scolopendria and Peperomia ponapensis; epiphytes Asplenium nidus, Nephrolepis acutifolia; lianas or creepers Ipomoea macrantha and WollastonIa biflora.

The proportions of the tree species vary locally, with a tendency to form groves or small areas of single species. Scattered coconut trees indicate that this forest, though probably close to the pre-human predominant type, has been subject to some human influence. Cut stumps, usually sprouting, point in the same direction.

A third local habitat described by Hatheway is termed Saline Flats. These are shallow depressions, with salt water reaching the surface at highest tides. These occur at least on Bikarej, Badrbaren, Namwi and Enidrl@ islets. They are completely dominated by Pemphis acidula, or in places lacking plant life altogether. Pemphis surrounds them on slightly higher exposed rock. This shrub or small tree can stand having its roots temporarily covered by sea-water.

In saline areas that are filled or covered by sand, Scaevola sericea and Tournefortia argentea mingle to some

extent with the Pemphis.

Pemphis also forms dense scrub-forests in other areas where bare limestone is exposed. This is the normal habitat for Pemphis in most parts of its range.

Mangrove swamps and what we now call mangrove depressions, the latter usually rock-bottomed, are fairly frequent on Arno, perhaps more so than in other Marshall atolls. The principal species is Bruguiera gymnorhiza, with slight to considerable representation of Sonneratia alba, Lumnitzera littorea and Pemphis acidula. Such swamps occur on Tinak, Langau, Bikarej and Manwi islets, the first two completely enclosed by sand or gravel ridges, the latter two connected with the sea. Swamps also occur at Kinajong and Matoleu districts on Ine Islet. Nephrolepis acutifolia and Asplenium nidus occur epiphytically on the mangrove trees. Elsewhere on the atoll are small local mangrove depressions, usually pure stands of Bruguiera, locally some Lumnitzera. Some of these stands may have resulted from Marshallese introduction of Bruguiera to wet places.

Hatheway also described fresh-water swamps or bogs, dominated by the "wild,' or small fruited form of Pandanus tectorius, called "erdwan" or "erwan" by the Marshallese. These are found on Ulien, Tutu and Arno islets. They may have been formed by successive storm ridges cutting off sections of reef flat. They have bottoms of fibrous peat. Other species of trees found occasionally are coconut, Hibiscus tiliaceus, Intsia bijuga, Morinda citrifolia, and Allophylus timoriensis. Epiphytes are Polypodium scolopendria, Nephrolopis acutifolia and Asplenium nidus. In more open places a herbaceous ground layer of Eleocharis geniculata, Thelypteris interrupta, and Polyoodium scolopendria occurs. Some such fresh-water swamps or marshes may have been taro or yaraj (Cyrtosperma) pits that were abandoned and invaded by the swamp trees and herbs.

Hatheway discusses the origin and dynamics of the secondary vegetation of Arno at length, interpreting most of it as following abandonment or failure of coconut plantings on poor or worn out land.

Lib Island

This island or table reef lies at 08° 19' N, 167° 25' E, south of Kwajalein. It has a large fresh-water pond in the eastern half, apparently containing some mangroves (Bruguiera ?). No scientific information is available, but I examined the island briefly from the air in 1960. It is inhabited and partly planted to coconuts. However, there is considerable native forest remaining on the north side

and around the pond. Tournefortia, Scaevola, Calophyllum, Pandanus, Hibiscus tiliaceus, Bruguiera, Artocarpus and Cocos, could be identified with some confidence from the air. This island would well repay a visit and careful study. I know of no collections of plants, birds, or other scientific specimens from Lib.

KWAJALEIN ATOLL

An enormous, roughly crescent-shaped atoll, said to be the largest in the world, 75 miles from tip to tip, about 30 miles wide at widest part, lying at 09° 05' N, 167° 20' E. This has been the U.S. military Pacific headquarters, a target area, and Western Pacific Headquarters of the Pacific Missile Range.

The reef periphery is almost 200 miles, with the 92 islets well-distributed with 3 large gaps. Kwajalein Islet, at the southern extremity is the largest, and is completely covered by the airport and installations. Most of the Marshallese population of tha atoll live on Ebeye Islet somewhat north of Kwajalein Islet on the east reef. The other large islets - the Roi-Namur complex and Ebadon, at the northern and western points, respectively, are very much altered, Roi-Namur by military installations, Ebadon by coconut planting.

The other almost 90 islets, with a few exceptions, are scientifically almost unknown. I have examined them all from the air several timas, from very favorable altitudes, taking notes. These islets are diverse in size and shape, as well as vegetation and position with respect to orientation and exposure to Trade Winds and waves. Most of the largest ones are more or less planted to coconuts, some partly wooded. A few of the smaller ones have some coconut trees, but most of the smaller ones seem to be in fairly natural condition, at least with spontaneous vegetation. Most are wooded or scrubcovered, or with grassy openings and open scrub. Much of the forest seems to be Piscnia, but with occasional patches of Neisosperma. Almost any of them seem well worth investigating. A very few of them have been visited by me many years back.

Perhaps the most important of these is Eniwetak Islet, not on the reef, but in the lagoon just inside the second passage from the south end of the east reef. This islet was in 1952 a magnificent forest of giant Pisonia grandis trees. On the ground was a thick layer of raw humus or mor, underlain by a continuous or somewhat fragmented layer of brown, white-speckled atoll phosphate rock. The only sign of disturbance was a small grove of coconuts on a slightly lower projection on the southeast side. I was told in 1965

that a small tower had been erected on this islet by the U.S. Pacific Missile Range personnel. Their commanding officer agreed to stop further use of the islet when its uniqueness and scientific importance were explained to him. In 1952 the islet was home of a very large sea-bird population. It seems possible that this was, in pre-European times, a Marshallese bird sanctuary, and that this tradition has protected it. If it is still intact, it should have the highest recommendation for a protected natural area.

Information was collected on several short visits to islets on the west reef, north of Kwajalein islets which may be of some interest.

Ligan Islet: This is really two islets connected by two dry land strips enclosing a fair-sized pond. The lagoonward side is convex and is a large rubble flat as long as the entire islet. Its outer 20 meters or so is consolidated rubble. The inner part is lower and not consolidated, scarcely dry at low tide. The seaward side of the isthmus is a double anticline-like series of beach-rock beds. The seaward sloping component extends along the entire seaward coast, but was partly destroyed by the Japanese construction of a seaplane ramp.

The north one of the two islets was briefly examined. There is a seaward fringe of Scaevola, then a strip planted to coconuts. In from this is a zone of Neisosperma forest, then old large Pisonia forest, being invaded by young Neisosperma. Between this and the lagoon is a tall scrub of Pemphis, Scaevola, Guettarda, Tournefortia and Terminalia. Birds of several species were common.

Enelapkan Islet is a north-west-southeast oriented islet, the central part planted to coconuts, but with a strip cleared for radio towers. The SE end is thickly wooded. The eastern extremity is a Pemphis forest of large trees (large for Pemphis), closed canopy, lower branches dead but persistent. This changes to a mixed forest of Guettarda, Pisonia, Neisosperma and Pemphis, the latter dropping out and Neisosperma becoming abundant, forming pure stands in places, with a dense ground cover of its seedlings. Intsia is common on the seaward side, more or less replacing Neisosperma, Ipomoea macrantha and Wollastonia biflora form tangles in the mixed forest.

On the northwest end is a scrub, dominated by Scaevola, mixed variously with Guettarda and Tournefortia tangled locally with Cassytha. In openings Thuarea and Lepturus form a grass cover. The scrub gets lower toward the extremity of the islet. On the seaward side the Scaevola

fringe is tall at the top of the beach, with some Guettarda and Tournefortia. On the seaward side of the northwest end is a tremendous series of beachrock.

MAJURO ATOLL

This is the present governmental headquarters, or capital, of the Marshalls Republic. It lies at 07° 09' N, 171° 12' E, is quite wet, has 57 islets, one of them half the length of the south reef. The islets of the eastern end and southern reef are connected by a paved road and causeways. The southern and eastern islets have practically no natural vegetation. Surprisingly nothing seems to be on record about the numerous north and northwest islets. They would repay a visit, which should be easy, as the headquarters of the field party will most likely be Majuro.

Fifteen species of birds are known from this atoll. Most of the weeds recorded from the Marshalls are, as might be expected, from Majuro and Kwajalein. There is seldom even a casual visit by a botanical observer that does not turn up a new weed record or two.

MALOELAP ATOL

This very large atoll lies at 08° 45' N, 171° 03' E. It is elongate-triangular in shape, 32 by 16 miles long and wide, and has 89 islets well distributed around the entire reef. It is rather wet, said to be more luxuriantly vegetated than most of the Marshalls, and supports a large human population. Scientific information on it is very scanty, almost nothing on vegetation, a few plant species recorded. Even the birds are scarcely known. Probably some of the smaller islets may still have natural vegetation, but most are certainly planted to coconuts. It should be visited if convenient, and collections made, but would scarcely justify a special trip.

JALUIT ATOLL

Jaluit is in some ways one of the best studied atolls in the Marshalls (except geologically). It was the headquarters of both German and Japanese administrations. It lies at 06° 00' N, 169° 35' E, and is a very large atoll, 30 miles long, 15 miles wide. On a short visit in 1946 I noted that the whole atoll seemed to be planted to coconuts and breadfruit. Only a few of the larger islets were seen then. Some of the smaller islets were still in more or less natural state, but not examined. Much of the pre-1946 information on the Marshalls was from observations and collections on Jaluit. The main islets were the sites of heavy bombardment and fighting in World War II.

In 1956 the atoll was hit by 3 typhoons in quick succession, the third Typhoon Ophelia, incredibly violent and destructive. Two Pacific Science Board expeditions, 1958 and 1960, visited the atoll to study the effects of these storms. The vegetation, both cultivated and natural, was devastated, especially on the southern and larger part of the atoll. The principal interest, scientifically, of this atoll, is now to study the processes of recovery from this damage. Unfortunately, after the 1960 study, this opportunity was neglected. There is no record of the recovery or even of the present status of the Jaluit ecosystem that seemed totally destroyed in 1958.

Two islets, Lijeron (Ledjiok) and Ribon, where the former in essentially unaltered condition before the storm, and the latter only partly planted to coconuts. Lijeron was probably a traditional bird and turtle reserve (Tobin 1952) in pre-European times and in recent times, even to 1958, regarded with a semi-superstitious awe, and usually avoided. Lijeron and part of Ribon were covered by dense Pisonia forest, with some large Intsia trees, and surrounded by a narrow zone of Tournefortia and Scaevola scrub and scrub-forest. The trees were mostly blown down by the storm, but, even by 1960, the areas were occupied by a dense stand of sprouts of Pisonia, 1-2 meters tall.

Jaluit would be well worth a visit, with special attention paid to at least these two tiny islets. Any description of present vegetation on Jabwor, Imruj, and Mejatto, the most affected by the typhoons would be of permanent value. In 1958 they were an incredible tangle of fallen trees, coconut trunks and broken stubs, criss-crossed as though by a tornado. In 1960 this was still the case, but many trees were either sprouting or putting out new branches.

On the NW extension of Lijeron was a pure stand of Pemphis, badly beaten by the storms, but still alive. Its present condition should be checked. Pemphis is a tree that is able to survive both wind beating and sea-water innundation.

Jaluit also has a greater development of mangrove swamps and depressions than are known from elsewhere in the group. In 1958 the trees, at least the dominant Bruguiera, were still standing but leafless and dead. In 1960 abundant seedlings were growing up between the bare poles. Their present status should be determined and described. Such swamps are present on at least Jabwor, Mejatto, Pinlap and Jaluit islets. Small mangrove depressions, rock-or sand-bottomed, are generally distributed.

The bird fauna of Jaluit is impressive, 33 species out of a total of 70 species known from the archipelago. Even in 1958, after the storms, there were thousands of birds flying over Lijeron Islet, which had probably long been their home.

JABWOT ISLAND

This tiny islet, only less than a quarter of a square mile, lies at 07° 47' N, 168° 59' E. It has no lagoon nor even a pond. It has been inhabited for some time and is generally planted to coconuts and breadfruit. It has not been scientifically studied, except for birds, of which 9 species are listed. I flew over it in 1960 and was able to identify with confidence *Scaevola*, *Tournefortia*, *Thuarea*, *Guettarda*, and cultivated coconut, breadfruit and papaya. It is surrounded by a band of native vegetation, narrow on three sides, broader on the other (east ?). It would be scarcely worth-while to make a special visit for biodiversity studies, but any observations would be new information.

RONGERIK ATOLL

Rongerik is a medium sized atoll, semi-dry, lying on 11° 21' N, 167° 26' E, with 5 principal islets and a number of smaller ones, wall distributed around the roughly circular reef, which has a large gap on the west side. This atoll was not considered habitable by the Marshallese, but the Bikini people were put there by the U.S. Navy to make way for the nuclear tests on Bikini. They were unable to subsist there, and had to be moved again. There are very few coconuts. Principal vegetation types on the larger islets are *Cordia* forest and mixed *Cordia* and *Pisonia*, with a continuous stand of *Pisonia* forest on the west end of Eniwetak Islet.

The only area studied, and very briefly, in 1956 was Eniwetak Islet, which was being much disturbed by construction of a radio station, involving bulldozing a strip across the center and a road the length of the seaward coast.

The *Cordia* and *Cordia-Pisonia* forests were in very poor shape, locally the *Cordia* was dead or nearly so. The soil in these forests is very peculiar, resembling only that found on Sifo Islet, Ailinginae. The upper horizon is a brown fluffy loam, underlain by a gray fine sand. Time was not available to prepare a proper sample or to describe the profile.

Twelve species of birds were seen during this short visit.

RONGELAP ATOLL

Rongelap Atoll, at 11° 20' N, 166° 50' E, is a large rather dry (60-70" rainfall) atoll, 30 x 23 miles, with a rather small population which was seriously affected by fallout from the Bravo hydrogen bomb explosion in 1954. It has a large number, said to be 58, of islets scattered on the north, southeast and south reefs, one tiny islet in the middle of the west reef.

Rongelap has a generally poor scrubby aspect, with forest, in places pure *Pisonia*, in poorer places *Guettarda* and *Tournefortia* changing to *Scaevola-Tournefortia* and *Scaevola* scrub, sloping and getting lower toward windward beaches. The better, darker soils are planted to coconuts, which are nowhere in very good conditions. The biggest plantation is on Rongelap Islet back of the village. But a large part of this islet is in poor mixed forest and scrub. The "elbow" of this islet is covered by a boulder-cobble ridge, with *Scaevola* scrub on the windward part, scattered bushes of *Scaevola*, *Tournefortia* and *Guettarda* to leeward.

Small islets seen from air have *Scaevola* scrub with scattered *Pisonia* and *Pandanus*. Some have a few poor coconuts. We actually landed on three, chosen to represent part of a logarithmic series of increasing intensities of fallout dosages from the "Bravo" blast in 1954 on Bikini Atoll to the west.

Eniwetak Islet has a double beach-ridge of sand, to 3-4 m high, back of the lagoon beach. Sandy areas have sparse coconuts, much grass, patches of *Cordia* and *Morinda*. Along the seaward side is *Scaevola* scrub with scattered *Pandanus*, edged with *Suriana*, most of it dead.

Kabelle Islet has a wide sand flat lagoonward of an old sand-ridge, with *Scaevola*, *Tournefortia* and *Guettarda* bushes, back of this flat coconut trees have a poor yellow appearance. In the central part is a rather loose *Pisonia* forest, surrounded by a scrub forest of *Guettarda*, *Scaevola* and small *Pisonia*. In the *Pisonia* forest is a rather poorly developed Jemo Soil, with 5-10 cm of humus. Lining the seaward beach is a rather open, wind-sheared and wind-grooved *Scaevola* scrub. Pumice pebbles are quite plentiful on the sand on this islet.

On Gegen Islet the seaward third is *Pisonia* forest, the rest of it is a scrub-forest of *Guettarda* and *Cordia*, with

Suriana that is completely dead, with a few isolated coconut trees. Back of the lagoon beach are two broad beach-ridges of sand and small gravel, with scattered shrubby vegetation. Between this and the scrub forest is a rather open mixed scrub of _Scaevola_, _Guettarda_ and _Cordia_.

At the time this atoll was visited, in 1956, most of the vegetation was in conspicuously poor condition, with only two of the species, _Scaevola sericea_ and _Tournefortia argentea_ appearing in normal healthy condition. _Pisonia_ was essentially leafless, possibly from previous dry weather, and flowering. It had clumps of dark.green leaves here and there that almost looked like mistletoe. The _Guettarda_ was partly dead and otherwise dying back from the tips. All other species were in clearly unhealthy shape, or dead.

This poor condition was suspected to be the result of cumulative effect of the radioactive fallout from the "Bravo" hydrogen bomb explosion 2 years earlier on Bikini. This islet had much the heaviest dose of radiation of any of the islets examined. If Rongelap can be visited by the biodiversity team, special attention should be paid to the condition of the vegetation on the four islets described above, to see if there has been reeovery or further deterioration in the 21 years that have elapsed. An observer in 1956 who had seen Gegen Islet in 1955 said that the vegetation appeared in much worse condition than in 1955. Another observer who examined it in 1957 and photographed places found that trees that were still living but in poor condition in 1956 were dead in 1957. It would be worthwhile to protect at least Gegen Islet from disturbance for long-term studies. Light might be thrown on the possibility of long delayed appearance of genetic changes due to ionizing radiation.

ERIKUB ATOLL

This medium-sized atoll lies at 09° 08' N, 170° 02' E, just south of Wotje Atoll, is 17 miles long and 5 wide, with a land area of only a third of a square mile. It has 14 islets, most of them near the southeast end of an oblong, NW-SE oriented reef. Erikub Islet, the largest, is mostly planted to coconuts. The atoll is uninhabited but is visited by Wotje Islanders who come to harvest copra. Nothing is on record as to the natural vegetation except unpublished notes of visits by Pacific Ocean Biological Survey personnel, not readily available. I flew over the atoll many years ago at a high elevation and remember that most of the islets, except Erikub, seemed to be relatively undisturbed. The birds are rather well-known, but any other information gathered would be new. This atoll would be well worth a visit by the Biodiversity Project team if practical.

UJELANG ATOLL

Ujelang is the westernmost of the Marshalls, lying at 09° 49' N, 160° 55' E, actually farther west than Kusaie, easternmost of the Carolines. Ujelang was considered one of the Carolines by early writers and administered from Ponape by the Germans. It is a medium sized atoll, roughly narrowly oblong, oriented NE-SW, 14 x 2-3.5 miles long and wide. Thirty-five islets are well-distributed on the reefs, the largest, Ujelang Islet, is at the south end of the northwest reef. Although this atoll traditionally belonged to the Eniwetak people, the Germans regarded Ujelang as government property and planted all the suitable parts to coconuts and managed it commercially. This practice may have been followed by the Japanese. The U.S. Administration, when Eniwetak was required for nuclear testing, moved the Eniwetak people to Ujelang. Recently, many, if not all, have been returned to Eniwetak when it was declared safe enough.

It is a somewhat moist atoll, with the larger islets well-vegetated, with some rather dry and grassy or scrub areas on small islets. Most of the available information on the natural history dates from a visit by the U.S. Geological Survey party in 1952.

Most of the land suitable for coconut culture was planted to coconuts by the Germans. Some of their plantings were on such rocky or saline ground that they did not do well. On many of the smaller islands only a few coconut trees were planted, perhaps experimentally. Most of these islets are very rocky, probably considered unsuitable for coconuts, and so are still covered by forest or scrub, or in some cases, grass and such creepers as _Triumfetta procumbens_. Some of the islets show boulder and cobble ridges and scoured areas with little soil or vegetation, regarded as the results of past typhoons.

Kalo Islet, at the northeast end of the southwest reef, is largely planted to coconuts, but with a strip of forest on seaward and northeast passage sides, mostly scrub forest of _Guettarda_, _Tournefortia_ and _Scaevola_. The plantation is neglected and has a tall thicket of _Pipturus_, _Pisonia_ and _Guettarda_ between the trees.

The next three islets, Kirinyon, Enimoni and Enilap are very rocky, largely covered by mixed forest of _Pisonia_, _Cordia_, _Guettarda_, _Allophylus_, and on outer parts, _Tournefortia_. Some coconut planting on lagoonward side, but neglected, overgrown, and in poor condition. Substantial areas on these islets are of coral conglomerate, swept clear

of soil, and covered by _Pemphis_ forest, often pure stands.

The islets on the northeast side of the atoll, from Bikan to Rais (Daisu) are very wind-beaten, partly wooded but with mixed scrub-forest or rather low _Pisonia_. _Pemphis_ on rock-surface. Kileken and Rais have been largely planted to coconuts.

On most of these smaller islets on both reefs are large bird populations. Some 15 species of birds were seen on this atoll, several in large numbers. Noddies, however, were being killed and eaten in some numbers in 1952.

Ujelang Islet, where most of the people live, is almost entirely planted to coconuts, except for the two ends and an enormous storm ridge along the seaward side, ends and ridge covered by scrub of _Scaevola_ and _Tournefortia_. The undergrowth in the plantation is mostly _Pipturus_.

In a shallow area in the lagoon off Ujelang Islet is a bed of turtle grass, _Thalassia hemprichii_, one of the few such in the Marshalls.

The vegetation of Ujelang is in general rather impoverished, though there is considerable area of at least spontaneous scrub and scrub forest. Curiously, _Neisosperma_ is either absent or rare. The atoll is scarcely worth a visit, except for the birds, and to determine present condition of the small islets, one or more of the less altered ones of which might be set aside as a protected natural area.

UJAE ATOLL

Ujae is an elongate diamond-shaped atoll, oriented NW-SE, lying at 09° 05' N, 165° 40' E, is 27 miles long, 8 miles wide at widest part, with 15 islets, the 3 largest at the ends and middle angle of the NE reef. The largest islets are mostly planted to coconuts, the smaller ones in something like original condition, with forest and scrub. Geomorphology and soils are diverse for an atoll, and have been studied in 1952, but detailed descriptions remain unpublished. The flora, of 61 known species, is large for an atoll. The climate is medium wet, 70-100 inches of rain annually.

Ujae Islet, largest islet and site of the village, is mostly planted to coconuts, locally with breadfruit, _Pandanus_, papaya and bananas. The outer and both passage shores are lined with a zone of scrub and scrub-forest, of the usual _Scaevola_, _Tournefortia_, _Morinda_, _Pandanus_, _Terminalia_, _Allophylus_; somewhat inland away from the beach,

<u>Pisonia</u>. A patch of <u>Pisonia-Guettarda</u> forest is somewhat inland from the southeast coast.

Coconuts are planted locally on most of the other islets in suitable soils, but, in 1952, these smaller plantations were rather invaded and overgrown by native wild species. The vegetation of the principal other islets is a mixed forest, rich in species, for an atoll forest, closed-canopy forests of 25-30 m stature, large trees. The largest, tallest trees are <u>Pisonia</u>, <u>Intsia</u> and <u>Neisosperma</u>, with, as lesser components, <u>Guettarda</u>, <u>Allophylus</u>, <u>Tournefortia</u>, <u>Pandanus</u>, <u>Terminalia</u>, <u>Ximenia</u>, <u>Cordia</u> and <u>Pemphis</u>. These trees occur in many proportions, combinations, densities and statures. Several of the species occur in significant pure stands, or dominant stands, describable and mappable as distinct vegetation types. Among these are <u>Pisonia</u> forest, <u>Intsia</u> forest, and <u>Pemphis</u> forest. These and the various facies of mixed broad-leaf forest occur in differing habitats, but the patterns are complex, possibly involving a component of chance.

Ujae has, for a coral atoll, a very complex geomorphology and a corresponding vegetation. The geomorphology shows much variation within the constraints of rather uniform chemical nature and geological history, the vegetation within the constraints of a rather uniformly wet environment with occasional temporary dry spells, and of a flora that is very limited as tropical floras go. There is no very definable pattern, though the geomorphic features and the vegetation types repeat themselves.

In 1952 the islets on Ujae were studied and described in more detail than were any other comparably wet atoll. These descriptions, a few sketch maps, and floristic features are recorded in my field notes, but to spell them out in this report would be repetitive and boring, as well as expensive.

I would strongly recommend that the team plan to spend some time on Ujae, with the view of preparing descriptions of some of the islets and determining any that should be placed in the planned protected area system. My descriptions are available for comparison, to indicate something of the dynamic status, both of the geomorphic features and of the vegetational features. I am not aware of any typhoon that has passed over Ujae in the 35 years that have elapsed, though the geology indicates typhoon effects previous to our 1952 visits.

One aspect meriting special mention as to 1952 condition and that would make desirable a 1988 resurvey is

the abundance of birds present, very unusual for an inhabited atoll. I observed the use of young black noddies for food, and was told that the people ate all of the kinds of birds except the reef heron, which "eats rats!" The following birds were seen in 1952 by me, not an expert ornithologist:

Great Frigate bird	Fregeta minor
Brown booby	Sula leucogaster
Red-footed booby	Sula sula
Common noddy	Anous stolida
Black or white-capped noddy	Anous tenuirostris
White or Fairy tern	Gygis alba
Black-naped tern	Sterna sumatrana
Crested tern	Thalasseus bergii
Pacific golden plover	Pluvialus dominica
Wandering Tattler	Heleroscelus incanum
Ruddy turnstone	Arenaria interpres
Bristle-thighed curlew	Numenius tahitensis
Whimbrel	Numenius phaeopus
Reef heron	Egretta sacra

A list of 14 species is not large, but the numbers, not counted, of course, were impressive.

An interesting behavioral feature, observed by my colleague, F.S. Macneil, was a noddy picking up an operculate snail, Nerita sp., flying with it to a considerable height, dropping it on a rock surface, following it down, and eating the animal from the broken shell. That this was not an exceptional behavior was shown by a large number of freshly broken Nerita shells scattered on the bare limestone surface of an erosion ramp.

Selected References on Marshall Islands Botany, Ecology and Geography

Following is a list of papers and books with information pertaining to the Marshall Islands and related topics that may be of interest in connection with the biodiversity investigation. Annotations for practically all items may be found in Island Bibliographies, by M. H. Sachet and F. R. Fosberg, 1955, and its supplement, 1971, National Academy of Sciences-National Research Council Publication 335.

Detailed field notes on various Marshall atolls may be found in the field note-books of F. R. Fosberg, by arrangement with him, Smithsonian Institution, Washington, D.C. The note-books will not be loaned.

This list does not, of course, exhaust the literature

that is available on coral atolls, or on the Marshall Islands. For example, there are well over 300 articles in the Atoll Research Bulletin (here abbreviated A.R.B.) many of which, more than listed here, may be of interest. The ones listed will document many of the statements in the present review, though much of what is said comes from personal experience and knowledge of the compiler.

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ATOLL RESEARCH BULLETIN

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AN ANNOTATED BIBLIOGRAPHY OF THE NATURAL HISTORY OF THE COCOS (KEELING) ISLANDS, INDIAN OCEAN

BY

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Introduction

This bibliography was prepared to assist scientists and managers to access the published work on the biota of the Cocos (Keeling) Islands. It has been based on several older selected reference lists as well as DIALOG database searching in 1987. Previous lists used were those of Gibson-Hill in his various publications and an unpublished bibliography compiled by D. R. Stoddart in 1976 which was based on listings in "Island Bibliographies" (edited by M-H. Sachet and F.R. Fosberg). A broader list, compiled by P. Bunce was also used.

The bibliography does not aim to be comprehensive as far as the taxonomy of the biota is concerned because of the impossibility of tracing relevant references where Cocos (Keeling) does not appear as an abstracting keyword. Unpublished work is largely excluded except for some few recent and relevant Departmental or consultant reports. Also excluded are newspaper, colonial government and minor historical reports which contain little mention of the biota. Gibson-Hill (ed. 1953) is most useful in regard to such reports.

Listings are in author, year, title order; together with annotation. There is a keyword index and an indexed list of first authors.

History of biota studies

It is clear from the bibliography that most work by scientists on Cocos has been stimulated by the extraordinary isolation of the atoll and thus its significance to the distribution of organisms. Cocos is not only one of the most remote atolls but it lies in a position which can be regarded as the western end of the Western Pacific marine biogeographic province. For many species, Cocos represents their westernmost limit of distribution.

There are other reasons why most studies have been restricted to collecting for taxonomic purposes. For one, many biologists have been there for only short periods and others were doing biological work as an adjunct to their professional work e.g. in medical practice. Access and the cost of getting to Cocos has hindered more detailed studies. Since the magnificent opportunistic efforts of Gibson-Hill in 1941 there have been only two major scientific efforts on Cocos until recently. Both were funded by North American agencies to enable collecting expeditions for fish (1974) and molluscs (1963).

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Despite the scientific interest in Cocos as a collecting locality, the biota has turned out to be unsurprising taxonomically. Unlike Christmas Island and the Aldabra atoll, Cocos has so far produced few endemic species. There is one endemic subspecies of bird (*Rallus phillipensis andrewsi*) and the introduced rat (*Rattus rattus keelingensis*). The *Pandanus* sp. on these islands is also currently being described as an endemic. All these are populations from widespread and very variable species so their distinctiveness on Cocos is not surprising. A few fish species are endemic here or at least have been collected only here. It is always likely that further collecting in other locations will increase the known distributional range of such species. However it is also likely that more intensive collecting on Cocos will find more endemics.

Plants

The major collections of land plants have been made by Darwin, (in 1836), Forbes (1879), Wood-Jones (1905), Jowett (1978), Telford (1985) and Williams (1986). The last collection covered every island and included island checklists and general vegetation patterns.

The flowering plant flora is being taxonomically reviewed for the Flora of Australia volume on Christmas and Cocos (Keeling) Islands, due for publication in 1990. So far, only one endemic species has been recognized. Given the degree of isolation of Cocos, this suggests the present land flora is relatively recent, perhaps largely post-glacial. The composition of the flora is as follows:

Growth Form	No. of Native Species	No. of Naturalized Species
Trees	17	7
Shrubs	9	8
Herbs	13	29
Grasses etc.	11	21
Seagrasses	3	-
Climbers	7	3
	60	68

About 40 species of marine algae and the relatively few lichens and mosses were collected by Williams in 1986 and these are being examined at the Australian National Botanic Gardens. The fungi have probably not been well collected, apart from some plant pathogens by Paton *et al.* (1981).

Invertebrates - Insects

Wood-Jones made the first attempt at a comprehensive insect collection in 1905. Unfortunately, many of the specimens collected by Gibson-Hill in 1941 went to Singapore and have not been located. Campbell (C.S.I.R.O.) made further collections in 1952 and 1964 and Paton *et al.* (1981) also collected insects and provided a checklist of their collection with most specimens identified at least to genus level. The Lepidoptera have been studied recently by Holloway (1982) who concluded that the moths and butterflies are largely native to Cocos, although there may have been a few introductions. Earlier authors have suggested that there have been many insect introductions since settlement.

Other Terrestrial Invertebrates

There has been only sporadic collecting of non-insect invertebrates and no work has been done on the soil fauna, although this does not appear to be diverse. Earthworms occur and are abundant during the wet season, probably contributing significantly to litter breakdown especially in husk piles. Soil nematodes (8 species) and litter molluscs (8 species) were recorded by Paton *et al.* (1981).

Invertebrates - Marine

The collections of Gibson-Hill were until 1989 the only recent ones for most marine invertebrates and in themselves were limited in coverage, for various reasons. His collections of soft corals, anemones, sea cucumbers, some starfish (Linckiidae) and worms were all lost during World War II. There are reasonable checklists for hard corals (74 species), echinoderms in part (30 species), molluscs (163 species, 154 marine) and crabs (c. 120 spp.); most of these published in the *Bulletin of the Raffles Museum* **22** (1950).

Maes (1967) collected the molluscs extensively in 1963 when two people collecting over 7 weeks yielded 486 species of molluscs from Cocos reefs and the lagoon, giving an overall 504 species. This total compared with the 154 species found by Gibson-Hill suggests that his collections of most groups are likely to be very inadequate.

The Western Australian Museum has this year completed a marine fauna survey for the Australian National Parks and Wildlife Service covering both invertebrates and fish.

Vertebrates - Terrestrial

Reptiles and birds have been the subject of considerable study over the years and there are recent publications on both groups. Cogger *et al.* (1983) summarized the past and present distribution of the four species of reptiles as well as their ecology and conservation needs. Stokes *et al.* (1984) provide the most recent checklist of bird species (31 approx.) with notes on distribution and breeding status with particular respect to North Keeling. All mammals on the Islands are introduced and there are no amphibians.

Vertebrates - Marine

The fish fauna was only sporadically collected until 1974 when a North American expedition visited. Many sites on the main atoll were sampled and SCUBA observations were made to depths of 75m. Several new species have been described based on Cocos specimens but unfortunately a full report on the collections has not been found and may not exist. There is a checklist for fishes of 189 species based on Gibson-Hill's 1941 collections, but this will be revised considerably by the recent survey. The only other marine vertebrates are the green and hawksbill turtles and an unidentified species of dolphin; all occur in and around the atoll. Apparently there are no resident sea snakes, although some have been found washed up.

North Keeling Island

Due to difficulty of access and related problems of collecting on North Keeling, this island has had only very occasional and limited collecting of its biota. Gibson-Hill visited for a total of 3 days in 1941 and gave a broad description of the various communities. Guppy in 1888 and Wood-Jones in 1906, each spent less than a day there and made only a brief account of their necessarily superficial observations. Since 1984, ANPWS officers have been surveying bird populations and in 1986 Williams surveyed the vegetation and flora and collected some marine algae.

Hence North Keeling is less well studied than the main atoll. Whilst one would not expect to find too many additions to the biota compared to the main atoll, there is a strong argument for documenting what is there now, in terms of North Keeling being a far less altered system than the main atoll. Fish, the marine and terrestrial invertebrates, and algae require most attention and are the groups most likely to produce additions to species lists.

Acknowledgement

The assistance of the Commonwealth Department of the Arts, Sport, the Environment, Tourism and Territories and of the Office of the Administrator of the Cocos (Keeling) Islands is gratefully acknowledged.

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Records the 154 species of marine and 9 land molluscs collected by Gibson-Hill. Brief notes on most species as to taxonomy and collection site on the main atoll.

Alfred, A.E. 1961. Some birds of the Cocos-Keeling Islands. *Malayan Nat. J.* **15**: 68-69.

Contains a list of bird species sighted during a visit of one month, without notes.

Anonymous 1830. Some account of the Cocos or Keeling Islands: and of their recent settlement. *Gleanings in Science* (Calcutta), 2(22), 293-301; repr. in. *J. Mal. Br. R. Asiatic Soc.(1952)* **25(4)**: 174-191.

An account of the settlement and its produce based on information available in official files and also provided by Ross.

Anonymous 1886. The Keeling Islands. *Proc. R. geog. Soc. N.S.* **8**: 263-265.

Presents a summary of a report on a visit in 1885 by E.W. Birch who was sent by the Governor of the Straits Settlements to report on the Islands.

Anonymous 1964. Insects on Cocos and public health. *Aust. Territories* **4(2)**: 24-25.

A general account based on the insect surveys of Campbell.

Anonymous 1984. Giant Clam Mariculture and other development possibilities on the Cocos Islands. Bureau of Agricultural Economics, Canberra. Unpublished.

This preliminary study concluded that clam mariculture on the Islands would be a high risk venture as much of the technology is yet to be proven.

Australia, Commonwealth Department of Housing and Construction 1986. Cocos (Keeling) Islands Coastal Management Report. D.H.C., Canberra.

Australia, Commonwealth Department of Territories and Local Government 1984. Self Sufficiency Study for Cocos (Keeling) Islands. Unpublished report by Cameron McNamara Consultants.

Detailed evaluation of horticulture, poultry production and alternative energy systems. Other options for development are considered briefly.

Barlow, N.(ed.) 1933. Charles Darwin's Diary of the Voyage of H.M.S. Beagle. Cambridge University Press..

A very similar account to The Voyage but with occasional differences that are useful in reconstructing events.

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Blake, B. & Blake, J. 1983. An account of events in the lagoon of Cocos (Keeling) atoll in March 1983. Unpublished report.

Reports an apparent bloom in the Cocos lagoon associated with a far southern excursion of the intertropic convergence zone. Home islanders say this has occurred two other times in living memory, but the 1983 one was worst. Water turned red, then yellow then brown. There had been a lot of rain and then NW winds, then calm.

Campbell, T.G. 1952. Entomological survey of Cocos (Keeling) Islands. Aviation Medicine Memorandum No.14. Dept. of Civil Aviation, Commonwealth of Australia.

Presents the results of a comprehensive insect survey. Methods of control of pests and

quarantine considerations are covered with respect to air travel from South Africa and Mauritius.

Campbell, T.G. 1964. Entomological survey of the Cocos (Keeling) Islands. CSIRO Division of Entomology, (unpublished).
Reports an entomological survey done during November 1964 and resulting in the collection of some 2,000 specimens. Reviews the origins of the insect fauna based on the records of previous collectors and discusses the insects of medical, veterinary, agricultural and timber significance. A full species list is given although not all species were fully identified.

Campbell, T.G. 1966. Mosquito Control - Cocos (Keeling) Islands. C.S.I.R.O. Division of Entomology, Unpublished Report.
Describes the habits of the three species found and recommends on suitable methods for their control around settlements.

Campbell, T.G. 1966. Rhinoceros beetle (*Oryctes rhinoceros* L.) in the Cocos (Keeling) Islands. 23pp. Dept. of Territories (unpublished).

Campion, H. 1923. Notes on dragonflies from the Old World islands of San Thome, Rodriguez, Cocos-Keeling, and Loo-Choo. *Ann. Mag. nat. Hist.* **(9)11**: 22-27.
Reports 3 species collected by Wood-Jones in 1906. *Pantula flavescens* Fabr., *Tramea rosenbergii* Brauer (*T. limbata* Desj.), and *Anax guttatus* (*A.(Hemianax) papuensis* Burm). The last apparently an Australasian species.

Chamberlain, N.G. 1960. Cocos Islands magnetic survey, 1946. B.M.R. Record 1960/124.
Reports measurement of the magnetic field associated with the Cocos atoll. These show the magnetic anomaly produced by the seamount on which these islands occur.

Chamisso, M. 1833. The Cocos Islands - Indian Ocean. *Naut. Mag.* **2**: 578-581.
An early record of the abundance of turtle, seabirds (very tame), robber crabs etc. on the main atoll.

Clark, A.H. 1950. Echinoderms from the Cocos-Keeling Islands. *Bull. Raffles Mus.* **22**: 53-67.
Records 15 sea urchins, 3 crinoids, 4 starfishes, and 8 brittle stars collected by Gibson-Hill. Does not include Holothurians nor starfish of the family Linckiidae.

Clarke, S. & Clarke, M.C. 1978. Cocos-Keeling cowries. *Aust. Shell News* **21**: 4-8.
Brief notes on some cowrie shell species.

Clarke, S. & Clarke, M.C. 1979. Cocos-Keeling cones - Part 1. *Aust. Shell News* **26**: 4-6.
Brief notes on some cone shell species.

Clarke, S. & Clarke, M.C. 1979. Cocos-Keeling cones - Part 2. *Aust. Shell News* **27**: 4-5.
Brief notes on some species of cone shells.

Cogger, H., Sadlier, R. & Cameron, E. 1983. The Terrestrial Reptiles of Australia's Island Territories. Special Publication 11. A.N.P.W.S., Canberra.
Describes the taxonomy, morphology, reproduction, thermal preferences, diet and habitat preferences of the three geckos and one blind snake found on Cocos. Aids to identification and distribution maps are included. Surveys were done in April/May 1979 and the raw data were deposited with ANPWS in separate reports.

Colin, P.L. 1977. The reefs of Cocos-Keeling atoll, Eastern Indian Ocean. Proceedings, Third International Coral Reef Symposium, pp. 63-68. Miami, Florida.

Describes the result of extensive diving in the northern lagoon and reef edge in 1974 as part of a fish-collecting expedition. Some profiles of the reef form are given and comment on the low cover of live hard corals generally. This was suggested as being possibly due to the Crown of Thorns Starfish and/or red tide phenomena. The last red tide was said to be about 1964.

Covacevich, J. 1983. The Cocos Islands. *Wildlife in Australia* **March**: 6-9.

A short popular article which emphasizes human impact on the flora and fauna since settlement.

Darwin, C. 1845. Journal of researches into the natural history and geology of the countries visited during the voyage of H.M.S. Beagle round the world, under the command of Capt. Fitz Roy, R.N.. London, John Murray.

Darwin, C. 1845. The Voyage of the Beagle..

Chapter 20 describes Darwin's general observations during the visit in April 1836. More specific treatment of some aspects is given in other publications by Darwin, Fitzroy, Henslow etc.

Darwin, C. 1889. The structure and distribution of coral reefs, being the first part of the geology of the voyage of the Beagle, under the command of Capt. Fitzroy, R.N. during the years 1832 to 1836. Smith, Elder and Co., London (3rd. ed.).

Chapter 1 Section first contains a description of the atoll's geology and origins based on the visit of 1836. Contains a reference to major fish kills in the lagoon about 1830, which was attributed to heavy rains and to some earth tremors in the preceding ten years.

Debelius, H. 1980. Mauritius, Maldives, Cocos (Keeling) Islands: the gap has been bridged for *Chaetodon mitratus*. *Tropical Fish Hobby*. **28(7)**: 87-98.

Diamond, A.W. 1985. The conservation of landbirds on islands in the tropical Indian Ocean. In: Conservation of Island Birds (ed. P.J. Moors) pp.85-100. ICBP Tech. Publ. No. 3.

Reviews the status of landbirds on all the major islands. Cocos is discussed with reference to Stokes *et al*. (1984). The only native landbird is the Cocos Buff-banded Rail (found only on North Keeling) and the only other species is the introduced Christmas Island Silver-eye found on Pulu Luar.

Feare, C.J. 1984. Seabird status and conservation in the tropical Indian Ocean. In: Status and Conservation of the World's Seabirds (eds. J.P. Croxall, P.G.H. Evans & R.W. Schreiber) pp. 457-471. International Council for Bird Preservation Tech. Publ. No. 2.

Reviews the conservation of 23 species of seabirds known to breeed on Indian Ocean islands. Habitat alteration is seen as presently the most damaging factor in relation to these birds, especially the boobies. Some islands are being allowed or encouraged to return to a more natural vegetation, due mainly to positive management for tourism.

Finlayson, D.M. 1970. First-order regional magnetic survey at Cocos Island, Southern Cross and Augusta. BMR Record 1970/101.

Reports measurement of the earth's magnetic field at Cocos.

Fitzroy, R. 1839. Narrative of the Surveying Voyages of His Majesty's Ships Adventure and Beagle, between the years 1826 and 1836, describing their examination of the southern shores of South America, and the Beagle's circumnavigation of the Globe. Volume II. H. Colburn, London.

Pages 628-638 describe observations made by Fitzroy during the Beagle's visit to Cocos.

Forbes, H.O. 1879. Notes on the Cocos or Keeling Islands. *Proc. R. geog. Soc.* **1**: 777-784.

Notes regarding Forbes' visit of 1879 when he specifically set out to compare changes in the Islands since Darwin's visit. Mainly observations about cyclone damage and presents a map showing areas of water discoloured in 1876 and coastline changes since 1836.

Forbes, H.O. 1885. A Naturalist's Wanderings in the Eastern Archipelago. A narrative of travel and exploration from 1878 to 1883. London, Sampson Row.

Chapters 2 & 3 Sojourn in the Cocos-Keeling Islands are relevant. Arrived about 17/1/1879 and left on 9/2/1879. Summarises the history of settlement including cyclone experiences, lagoon phenomena related to a possible earth tremor, crabs, plants, insects, birds, atoll formation and geomorphology. Cross references to Darwin's work. Contains a detailed map, list of plants and birds and a few coral species collected.

Forest, J. 1956. La faune des Iles Cocos-Keelings, Paguridea. *Bull. nat. Mus. Singapore* **27**: 45-55.

Describes, in French, 16 species of marine intertidal hermit crabs collected by Gibson-Hill.

Fosberg, F.R. 1956. Disposition of *Urera gaudichaudiana* Henslow. *Ann. Mag. Nat. Hist.* Ser. 12, **ix**: 423-424.

Describes the taxonomic status of the specimen collected by Darwin now referred to *Laportea aestuans*, a widespread weedy American species also found in scattered localities in Africa.

Gibson-Hill, C.A. 1947. Field notes on the terrestrial crabs. *Bull. Raffles Mus.* **18**: 43-52.

Relates to Christmas Is. species but some relevance to Cocos. Brief notes on *Gecarcoidea humei*, *Cardisoma hirtipes*, *Geograpsus grayi* and *Birgus latro*.

Gibson-Hill, C.A. 1947. Notes on the Cocos-Keeling Islands. *J. Mal. Br. Roy. Asiatic Soc.* **20(2)**: 140-202.

Excellent socio-historical account of the Islands up to 1941. Includes notes on Cocos-Malay culture, including their use of plants and animals. Appendices cover the *de facto* owners to 1944, selected bibliography, cyclones and Cocos-Malay words referring to dress and housing.

Gibson-Hill, C.A. 1948. The island of North Keeling. *J. Malay. Br. Roy. Asiatic Soc.* **21(1)**: 68-103.

The only detailed study of the island prior to 1986, other than that of Guppy, who spent 6 days on the island in 1888. Contains description of the vegetation (with a map), associated seabirds and other fauna, history of use by the islanders. Several appendices cover the name 'Cocos-Keeling', the wreck of the 'Emden', and a faunal species checklist. Plates and Maps.

Gibson-Hill, C.A. 1948. The robber crab. *Malayan Nature J. (Kuala Lumpur)* **3(1)**: 10-14.

(also published in Zoo Life, 4, 1949, 58-60). Contains some broad observations on the robber crab based on work on Cocos and Christmas Islands. Hunting for food is said to be the major cause of the species decline in abundance on Cocos. This crab generally hides under rock ledges or fallen trees and was not observed to make serious attempts to dig its own burrow. Discusses the coconut opening ability of the crab.

Gibson-Hill, C.A. 1949. Boats and fishing on the Cocos-Keeling Islands. *J. R. anthr. Inst. Gt. Brit.* **76(1)**: 13-23.

Describes boat construction, methods of fishing, major species and locations, giving scientific and local names. Also covers preparation of the catch. Useful regarding traditional conservation methods and provides some quantitative catch data. Glossary of sailing and fishing terms including wind and sea conditions and lagoon habitats.

Gibson-Hill, C.A. 1949. The birds of the Cocos-Keeling Islands (Indian Ocean). *Ibis* **91**: 221-243.
Describes the islands in general and contains an annotated checklist of species including breeding species and vagrants in 1941. Previous records are analyzed and comparison is made with the avifauna of Christmas Island. Some estimates of numbers breeding.

Gibson-Hill, C.A. 1950. A note on the Arachnida found on the Cocos-Keeling Islands, January-October, 1941. *Bull. Raffles Mus.* **22**: 101-102.
Brief record of arachnids, specimens of which were lost in the war. One scorpion, *Isometrus maculatus* is known locally as Kala Jengking. 23 spiders and 2 ticks were also collected.

Gibson-Hill, C.A. 1950. A note on the Cetacea stranded on the Cocos-Keeling Islands. *Bull. Raffles Mus.* **22**: 278-279.
Records two whale species found on the atoll, the Sperm Whale and possibly the Indian Pilot Whale.

Gibson-Hill, C.A. 1950. A note on the Cocos-Keeling Islands. *Bull. Raffles Mus.* **22**: 11-28.
A good general account of the islands' history, climate, geomorphology and biology, including North Keeling. An appendix lists the *de facto* owners of the islands, recorded cyclones (1862 - 1909) and a selected bibliography of the main original works relating to the Cocos Islands.

Gibson-Hill, C.A. 1950. A note on the reptiles occurring on the Cocos-Keeling Islands. *Bull. Raffles Mus.* **22**: 206-211.
Brief descriptions of morphology and distribution of 2 turtles, 3 geckoes and a blind snake.

Gibson-Hill, C.A. 1950. Hemiptera collected on the Cocos-Keeling Islands, January-October 1941. *Bull. Raffles Mus.* **23**: 206-211.
An annotated list of species collected.

Gibson-Hill, C.A. 1950. Notes on the birds of the Cocos-Keeling Islands. *Bull. Raffles Mus.* **22**: 212-270.
Comprehensive descriptions of the morphology and biology of the birds with an annotated checklist.

Gibson-Hill, C.A. 1950. Notes on the insects taken on the Cocos-Keeling Islands. *Bull. Raffles Mus.* **22**: 149-165.
Extensive notes on only a few of the orders. Also gives a history of insect collections of Cocos.

Gibson-Hill, C.A. 1950. Papers on the fauna of the Cocos-Keeling Islands. Based on material and data collected in the group by C.A. Gibson-Hill, M.A., between December 1940 and November 1941. Introduction. *Bull. Raffles Mus.* **22**: 7-10.
Gibson-Hill introduced this set of papers based on his collections. Describes previous visits by naturalists and the taxa whose collections were lost during the war. Local names for species are given in all of these papers.

Gibson-Hill, C.A. 1950. The Myriapoda found on the Cocos-Keeling Islands January-October 1941. *Bull. Raffles Mus.* **22**: 103-104.
Brief record of 4 centipedes and 2 milipedes, most not identified.

Gibson-Hill, C.A. 1951. The Cocos-Keeling Islands. *Geogr. Mag.* **24**: 313-317.
A popular article describing the history and people of Cocos.

Gibson-Hill, C.A. (ed.) 1953. Documents relating to John Clunies Ross, Alexander Hare and the settlement on the Cocos-Keeling Islands. *J. Mal. Br. R. Asiatic Soc.* **25(4)**: 1-306.

A most useful compendium of older (pre 1860), and more difficult to obtain reports and letters concerning the subject. Some of the earlier reports are relevant to considerations of the pre-settlement biota.

Gould, J. 1838-41 1841. Birds. In: The zoology of the voyage of H.M.S. Beagle: 3. (ed C.R. Darwin) pp. 1-159. London, Smith Elder.

Guppy, H.B. 1889. The Cocos-Keeling Islands. *Scot. Geog. Mag.* **5**: 281-297.
Parts II and III are on pages 457-474, 569-588.
Guppy stayed on the islands for ten weeks from Aug-Sept. 1888. He examined every island and islet and the lagoon. His account mainly considers the process of atoll formation and the geomorphology of the islands. Many detailed observations on corals were recorded together with a description of North Keeling, an 'island never before visited by a naturalist'. There are descriptions of each and all of the islands and of the lagoon.

Guppy, H.B. 1890. The dispersal of plants as illustrated by the flora of the Keeling or Cocos Islands. *J. Trans. Victoria Inst. London*, **24**: 267-306.
A very detailed account of the flora with reference to drift species, Darwin's collection and the flora records of Ross and Jagt which were made in 1829-30. Establishes the likelihood of species being in the indigenous flora.

Guppy, H.B. 1890. Preliminary note on the Keeling Atoll. *Proc. Vict. Inst.* **23**: 72-78.

Harms, J.W. 1933. Bericht ueber eine Reise nach Christmas- und Cocos- Island von Dezember 1932 bis Juni 1933. *Biologe, Munchen* **2(13)**: 301-306.

Hawson, M.G. 1985. The Potential for Horticultural Production Cocos (Keeling) Islands. Department of Agriculture, W.A. Unpublished report.
A detailed study of the costs and benefits of intensive horticulture of selected species on Cocos.

Henslow, J.S. 1838. Florula Keelingensis. An account of the native plants of the Keeling Islands. *Mag. Nat. Hist.* **1**: 337-347.
Based on Darwin's collection done in 1836. Twenty one indigenous species collected (including a moss and a fungus) and two others referred to; probably *Pisonia* and *Barringtonia*. Notes on each species indicate aspects of its taxonomy, distribution and ecology. *Barringtonia* was said to be 'a single tree'.

Hill, A.W. 1929. The original home and mode of dispersal of the coconut. *Nature* **124**: 133-153.
Refers to the early observations of naturalists with respect to the presence and dispersal of the coconut on Cocos (Keeling).

Holloway, J.D. 1982. On the Lepidoptera of the Cocos-Keeling Islands in the Indian Ocean, with a review of the *Nagia linteola* complex (Noctuidae). *Entomologia Gen.* **8(1)**: 99-110.
Provides a systematic account of the 59 species of Lepidoptera that have been recorded. The *Nagia linteola* complex of species is reviewed and the paper gives a review of the biogeography of the Cocos Lepidoptera. Most species are said to have colonized naturally with only a few possible exceptions.

Holman, J. 1840. Travels in China, New Zealand. London, 2nd edition, 4 vols. [On Cocos-Keeling, vol. 4, 374-388].

Izzard, R.J. 1959. A new species of *Nysius* (Hemiptera, Heteroptera: Lygaeidae) from Cocos Keeling and Canton Is. *Entom. Mon. Mag.* **94**: 285-286.

Jacobson, G. 1976. Preliminary investigation of groundwater resources, Cocos (Keeling) Islands. B.M.R. Record 1976/64.

Contains much of the field data gained during these investigations, including descriptions of all wells on Home Island.

Jacobson, G. 1976. The freshwater lens on Home Island in the Cocos (Keeling) Islands. *BMR J. Aust. Geol. Geophys. (Canberra)* **1/4**: 335-343.

Measurements of water levels in wells and comparison with tidal levels indicate a theoretical freshwater lens up to 19 m thick and averaging 15 m over an area of 30 ha. The sustainable yield of the aquifer is estimated at 0.2 Ml per day.

Jongsma, D. 1976. A review of the geology and geophysics of the Cocos Islands and Cocos Rise. *Bureau of Mineral Resources, Australia, Record 1976/38* .

The Cocos Islands lie in the northeast Indian Ocean on a northeasterly-trending line of seamounts termed the Cocos Rise. The islands consist of coral reefs built on a basaltic volcano which rises from a depth of about 5000 m with a gradient of 0.2. To the south lies the Umitaka Mary seamount which rises to 16 m from the sea surface. Sediments on the Cocos Rise are very thin, ranging from 100 to 200 m thick. Several figures present a. the sediments and bedrock in the region obtained in three bores done by the Glomar Challenger during the Deep Sea Drilling Project; b. a tectonic summary of the Eastern Indian Ocean and; c. the bathymetry around Cocos. (More recent bathrymetric surveys put the Umitaka seamount at 135 km SW and with a depth of about 22 m over an area of about 4 sq. km.)

Keating, A. S. 1840. Account of Cocoas or Keeling's Islands. In Travels in China, New Zealand. J. Holman. (London, 2nd edition), pp. 374-385.

Maes, V. 1967. The littoral marine mollusks of Coços-Keeling Islands (Indian Ocean). *Proc. Acad. Nat. Sci. Phil.* **119**: 93-215.

Lists 504 species either collected in 1963 or cited by Abbott (1950). Collecting localities and commoness are noted. Many photographs are given as well as reference to illustrations in Japanese texts.

Mangles, - 1840. Notes on Cocoas or Keeling's Islands. In Travels in China, New Zealand. J. Holman. (London, 2nd edition), pp. 385-388.

Marlow, B.J. 1970. A record of a Mastiff Bat, *Tadarida plicata*, from the Cocos (Keeling) Islands. *Extrait de Mammalia* **34**

Marrat, F.P. 1879. Notes on shells from the Keeling or Cocos Islands, Indian Ocean. *Proc. Lit. Philos. Soc. Liverpool* **33**: iii-iv.

Marsh, T.D. 1948. Visit to Cocos-Keeling Islands and Christmas Island. *Malay. agric. J.* **31**: 143-.

A short note which states that "the object of Mr. Marsh's visit to the Cocos-Keeling Islands was to enquire into the agricultural economy of the islands with a view to suggesting how it might be extended by crops alternative to coconuts and the development of derived products. The question of the raising of poultry for the Singapore market was also to be investigated."

Marshall, N.B. 1950. Fishes from the Cocos-Keeling Islands. *Bull. Raffles Mus.* **22**: 166-205.

Records 189 species, one of these being a new species of *Scorpaenodes* and 119 being new records for Cocos. Excellent notes on colour and ecology provided by Gibson-Hill.

Moorhouse, S. 1947. The Cocos Islands. *Canad. Geog. J.* **34**: 86-89.
A general account of the settlement etc.

Murray, M.D. & Marks, E.N. 1984. Blood-sucking Diptera of the Cocos (Keeling) Islands. *J. Aust. ent. Soc.* **23**: 265-268.
Three species of mosquitoes, *Aedes albopictus*, *Culex sitiens* and *C. quinquefasciatus* (= *fatigans*) were collected in Sept. 1980. Previous records of mosquitoes, their habits, breeding places, medical importance and possible control measures are discussed. *A. albopictus* breeds opportunistically in fresh water, *C. sitiens* breeds in brackish and salty situations.

Owen, E.W.C.R. 1831. Account of the Cocos, or Keeling Islands. *J. R. geog. Soc.* **1**: 66-69.
A useful early account of the flora and fauna including the early introductions. Trees noted were the coconut, *Cordia, Terminalia, Hernandia, Pisonia, Hibiscus, Erythrina, Morinda*. 'Two species of gannet and the frigate bird are particularly numerous about these islands ... turtles are very numerous and may be caught, without difficulty, in all seasons'.

Paton, R., Navaratnam, S.J. & Khair, G. 1981. Pest and disease survey, Cocos (Keeling) Islands. Unpublished report. Dept. of Primary Industry, Canberra.
Records the results of a survey in July 1981 to examine pest and disease potential prior to the opening of the quarantine station. Many species lists provided but not all fully identified. They cover plant pathogens, weeds, nematodes, snails and insects.

Proctor, D.M. 1986. Charles Darwin's vascular plant specimens from the voyage of H.M.S. Beagle. *Bot. J. Linn. Soc.* **93**: 1-172.
This compendium gives the current names for the specimens collected by Darwin.

Randall, J.E. 1975. A revision of the Indo-Pacific angelfish genus *Genicanthus*, with descriptions of three new species. *Bull. Mar. Sci.* **25(3)**: 393-421.
A taxonomic paper which, among other things, describes the new species *G. bellus* from Cocos and Tahiti. The species is named bellus from Latin for beautiful as it is the most colourful in the genus.

Randall, J.E. 1980. Revision of the fish genus *Plectranthias* Serranidae Anthiinae with descriptions of 13 new species. *Micronesica* **16(1)**: 101-187.

Randall, J.E. and Lubbock, R. 1981. A revision of the Serranid fishes of the subgenus *Mirolabrichthys* Anthiinae Anthias with descriptions of 5 new species. *Contrib. Sci. (Los Ang.)* **333?**: 1-28.

Randall, J.E. and Smith, M.M. 1982. A review of the Labrid fishes of the genus *Halichoeres* of the Western Indian Ocean with descriptions of six new species. *Ichthyol. Bull. J.L.B. Smith Inst. Icthyol.* **45**:1-25.

Randall, J.E., Matsuura, K., & Zama, A. 1978. A revision of the Riggerfish genus *Xanthichthys*, with a description of a new species. *Bull. Mar. Sci.* **28(4)**: 688-706.
A taxonomic paper which records *Xanthichthys auromarginatus* The Gilded Triggerfish from Cocos based on the 1974 Academy of Natural Sciences of Philadelphia Expedition to Cocos. The species was found on the outer reef from 12 to 46 m depths. In Hawaii this species appears to eat exclusively zooplankton, mainly calanoid copepods.

Rees, W.J. 1950. The cephalopods of the Cocos-Keeling Islands collected by C.A. Gibson-Hill. *Bull. Raffles Mus.* **22**: 99-100.
Records a nautilus, squid and octopus collected by Gibson-Hill. Names given.

Renvoize, S.A. 1979. The origins of Indian Ocean floras. In Plants and Islands (ed. D.Bramwell). Chapter 7 pp107-129. Academic Press, London.

Considers the origins of floras in relation to their geological history and proximity to sources of immigration, along with the major mechanisms of plant dispersal. Discussion of Cocos (Keeling) is based on Wood-Jones (1912).

Ross, J.C. 1836. On the formation of the oceanic islands in general, and of the coralline in particular. Singapore Free Press, 2 June 1836; repr. in. *J. Mal. Br. R. Asiatic Soc.(1952)* **25(4)**: 251-260.

A rather prolix discussion on the mechanisms of coral island formation, including the development of seamounts and the processes of sediment accumulation to form the cay.

Ross, J.C. 1855. Review of the theory of coral formations set forth by Ch. Darwin in his book entitled: Researches in Geology and Natural History. *Natuurk. Tidschr. voor Nederl. Indie.* **8**: 1-43.

Contains a counterpointed review of Darwin's arguments for the means by which his various classes of reefs are formed.

Ross, J.C. 1919. Papers 1821-1854. British Museum Add. 37631; 233 folios.

Roth, B. 1972. A new species of *Pugnus* from Cocos Keeling Islands Indian Ocean. *Bull. South Calif. Acad. Sci.* **71(2)**: 106-107.

Russell, R.J. and McIntire, W.G. 1965. Southern hemisphere beach rock. *Geogrl. Rev.* **55**: 17-45.

Describes the nature and origins of beach rock based on observations in the tropical Indo-Pacific. Field work included five days on West Island in 1963 and there is one page devoted to Cocos specifically. It is suggested that coastal retreat is not as rapid as local opinion would have, but that it is evident that many changes in strandline position are under way.

Slocum, J. 1899. Sailing Alone around the World.

Chapter XVI refers to the visit to Cocos in July 1897. General description of the settlement. Mentions taking 30 clams on board to replace 3 tons of cement ballast.

Smith, T.E. 1960. The Cocos-Keeling Islands: a demographic laboratory. *Pop. Stud.* **14**: 94-130.

A demographic analysis of births, deaths and marriage records from 1888 to 1947 by a former Administrator (1946-7). Observations on the historical and social background are made as well as on the registration procedures used during the period. Marriage, divorce, widowhood, mortality (esp. infant), fertility and abortion are discussed in the context of the life table developed.

Smith-Vaniz, W.F. and Randall, J.E. 1974. Two new species of angelfishes (*Centropyge*) from the Cocos-Keeling Islands. *Proc. Acad. Nat. Sci. Phil.* **126(8)**: 105-113.

Describes two species of deep water habitats.

Stokes, T. & Goh, P. 1987. Records of Herald Petrels and the Christmas Frigatebird from North Keeling Island, Indian Ocean. *Australian Bird Watcher* **12**: 132-133.

Reports two additional species for the checklist of North Keeling Island.

Stokes, T., Sheils, W. and Dunn, K. 1984. Birds of the Cocos (Keeling) Islands, Indian Ocean. *Emu* **84**: 23-28.

The birds of the islands were surveyed in January 1982 and analysed along with other records. Thirty four species are recorded, of which nine are new records. Three species, introduced between 1885-1906 and recorded in 1940-41 or 1958, are believed to be extinct. Very few land or sea birds now occur on the main atoll.

Tate, O.H. 1950. The Muridae of the Cocos-Keeling Islands. *Bull. Raffles Mus.* **22**: 271-277.

Describes the various rats on Cocos and the history of their introduction as far as it is known. The Direction Island race is described as a subspecies *R. r. keelingensis.*

Tweedie, M.W.F. 1950. The fauna of the Cocos-Keeling Islands, Brachyura and Stomatopoda. *Bull. Raffles Mus.* **22**: 105-148.

Records the crabs and stomatopods collected by Gibson-Hill. Extensive notes on some species and some figures. Probably a very representative collection of the littoral and terrestrial fauna.

Urquhart, A.W. 1960. Cocos (Keeling) Islands, Indian Ocean - a library summary. California, Point Mugu, Pacific Missile Range. 26 pp.

A summary of all aspects of the islands based on published material to 1960. Broadly covers ecology, social apsects, transport and communications.

Van der Jagt, H. 1831. Beschrijving der Kokos - of Keeling-Eilanden. Verh. Batav. Gen. v. Kunsten en Wetenschappen (Batavia), 13, 293-322; trans. in. *J. Mal. Br. R. Asiatic Soc.(1952)* **25(4)**: 148-159.

An early (1829) firsthand description of the islands and their natural resources. Mention is made of coconut production, turtles, native plants, vegetation etc.

Vaughan, T.W. 1918. Some shoal-water corals from Murray Island, Cocos-Keeling Islands, and Fanning Island. Carnegie Inst. Wash. Pub. 213, pp.49-234.

The first extensive discussion of the corals of Cocos based on the collections of Wood-Jones.

Waterman, S.A. 1975. The jukongs of Cocos-Keeling. *Oceans* **8(1)**: 36.

Wells, J.W. 1950. Reef corals from the Cocos-Keeling atoll. *Bull. Raffles Mus.* **22**: 29-52.

Gibson-Hill's collection bring the total number of species of hard corals to 74 and genera to 24. A checklist is provided and gives the collectors and habitats. Detailed morphological notes for many species, some plates and distribution data outside Cocos are given.

Wood Jones, F. 1909. The fauna of the Cocos-Keeling Atoll, collected by F. Wood Jones. *Proc. zool. Soc.* **1909**: 132-160.

This reports the species found in 1905-6 over 15 months. Descriptive notes provided on most species as well as Malay names. Identifications were mostly done by others and these parts of the paper are sometimes quoted as separate publications by them.

Wood-Jones, F. 1909. The coral island question. *Proc. zool. Soc* **1909**: 671-679.

Wood-Jones, F. 1912. <u>Coral and Atolls: a history and description of the Keeling-Cocos Islands, with an account of their fauna and flora, and a discussion of the method of development and transformation of coral structures in general</u>. Lovell Reeve & Co., London.

A classic book on the islands' natural history. The subtitle indicates the range of topics covered - their history, description, theories of their origin both before and since that of Darwin, the influence of winds, tides and ocean currents on their formation and transformations, their present condition, products, fauna and flora. Appendices are annotated checklists of the flora and fauna.

KEYWORD INDEX

E.W.C.R. 1831; Paton, R., Navaratnam, S.J. & Khair, G. 1981; Randall, J.E. 1975; Randall, J.E. 1980; Randall, J.E. and Lubbock, R. 1981; Randall, J.E. and Smith, M.M. 1982; Randall, J.E., Matsuura, K., & Zama, A. 1978; Rees, W.J. 1950; Roth, B. 1972; Smith-Vaniz, W.F. and Randall, J.E. 1974; Stokes, T. & Goh, P. 1987; Stokes, T., Sheils, W. and Dunn, K. 1984; Tate, O.H. 1950; Tweedie, M.W.F. 1950; Urquhart, A.W. 1960; Van der Jagt, H. 1831; Vaughan, T.W. 1918; Wells, J.W. 1950; Wood Jones, F. 1909; Wood-Jones, F. 1912.

FISH

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FLORA

Barlow, N.(ed.) 1933; Beccari, 0. 1917; Darwin, C. 1845; Darwin, C. 1845; Fitzroy, R. 1839; Forbes, H.O. 1885; Fosberg, F.R. 1956; Gibson-Hill, C.A. 1947; Gibson-Hill, C.A. 1948; Gibson-Hill, C.A. 1950; Gibson-Hill, C.A. (ed.) 1953; Guppy, H.B. 1889; Guppy, H.B. 1890; Henslow, J.S. 1838; Owen, E.W.C.R. 1831; Paton, R., Navaratnam, S.J. & Khair, G. 1981; Proctor, D.M. 1986; Renvoize, S.A. 1979; Urquhart, A.W. 1960; Van der Jagt, H. 1831; Wood-Jones, F. 1912.

GECKO

Cogger, H., Sadlier, R. & Cameron, E. 1983; Gibson-Hill, C.A. 1950.

GEOLOGY

Barlow, N.(ed.) 1933; Chamberlain, N.G. 1960; Darwin, C. 1845; Darwin, C. 1889; Finlayson, D.M. 1970; Jongsma, D. 1976.

GEOMORPHOLOGY

Colin, P.L. 1977; Forbes, H.O. 1885; Gibson-Hill, C.A. 1950; Guppy, H.B. 1889; Ross, J.C. 1836; Ross, J.C. 1855; Russell, R.J. and McIntire, W.G. 1965; Stoddart, D.R. 1985; Wood-Jones, F. 1909; Wood-Jones, F. 1912.

GROUNDWATER

Jacobson, G. 1976; Jacobson, G. 1976.

HOME ISLAND

Gibson-Hill, C.A. 1951.

INSECTS

Anonymous 1964; Campbell, T.G. 1952; Campbell, T.G. 1964; Gibson-Hill, C.A. 1948; Gibson-Hill, C.A. 1950; Gibson-Hill, C.A. 1950; Izzard, R.J. 1959; Murray, M.D. & Marks, E.N. 1984; Paton, R., Navaratnam, S.J. & Khair, G. 1981; Wood Jones, F. 1909.

ISLANDS

Renvoize, S.A. 1979; Russell, R.J. and McIntire, W.G. 1965; Wood-Jones, F. 1909; Wood-Jones, F. 1912.

MANAGEMENT

Anonymous 1984; Australia, Commonwealth Department of Territories and Local Government 1984; Campbell, T.G. 1966; Department of Housing and Construction 1986; Gibson-Hill, C.A. 1949; Hawson, M.G. 1985.

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Abbott, R.T. 1950; Clarke, S. & Clarke, M.C. 1978; Clarke, S. & Clarke, M.C. 1979; Clarke, S. & Clarke, M.C. 1979; Maes, V. 1967; Marrat, F.P. 1879.

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Campbell, T.G. 1966; Murray, M.D. & Marks, E.N. 1984.

NORTH KEELING

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Colin, P.L. 1977; Darwin, C. 1845; Darwin, C. 1889; Stoddart, D.R. 1985.

REPTILES

Cogger, H., Sadlier, R. & Cameron, E. 1983; Gibson-Hill, C.A. 1950; Wood Jones, F. 1909.

SEABIRDS

Feare, C.J. 1984; Gibson-Hill, C.A. 1948; Stokes, T. & Goh, P. 1987; Stokes, T., Sheils, W. and Dunn, K. 1984.

SETTLEMENT

Anonymous 1830; Anonymous 1886; Barlow, N.(ed.) 1933; Barrow, J. 1832; Chamisso, M.1833; Darwin, C. 1845; Fitzroy, R. 1839; Forbes, H.O. 1885; Gibson-Hill, C.A. 1947; Gibson-Hill, C.A. 1950; Gibson-Hill, C.A. 1951; Gibson-Hill, C.A. (ed.) 1953; Guppy, H.B. 1889; Marsh, T.D. 1948; Moorhouse, S. 1947; Owen, E.W.C.R. 1831; Slocum, J. 1899; Urquhart, A.W. 1960; Van der Jagt, H. 1831.

VEGETATION

Gibson-Hill, C.A. 1948; Gibson-Hill, C.A. (ed.) 1953; Guppy, H.B. 1889.

YACHTS

Slocum, J. 1899; Waterman, S.A. 1975.

AUTHOR INDEX

ATOLL RESEARCH BULLETIN

NO. 332

VEGETATION AND FLORISTICS OF THE TONGATAPU OUTLIERS

BY

JOANNA C. ELLISON

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VEGETATION AND FLORISTICS
OF THE TONGATAPU OUTLIERS

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JOANNA C. ELLISON

Abstract

On the 21 small islands located within the northern bays and reef systems of Tongatapu, Tonga, species of terrestrial flora present were identified, and vegetation units and gemorphological features surveyed on 12 that were previously unmapped. A species/ area plot of the data shows that rock islands are consistently more diverse than sand islands. Size of flora is also a function of frequency of human use of islands, which increases with area, and proximity to the mainland. Floristic composition varies from east to west across the group, with increasing shelter provided by the mainland from prevailing winds.

Introduction

Tongatapu is the largest of a group of islands that form the Kingdom of Tonga in the southwest Pacific (Latitude 21°08'S, Longitude 175°11'W). The island has an area of 245 km^2, with a maximum dimension of 35 km from east to west. It is composed of raised Quaternary limestone (Taylor & Bloom 1977), with a low undulating topography. The cliffed south coast is fringed by a raised algal ridge (Ladd & Hoffmeister 1927), while the leeward north shore is fringed by mangroves and discontinuous barrier reefs.

In association with this reef system 21 islands of 0.008 to 51.8 ha. (0.02 to 128 acres) occur to the north of Tongatapu (Figure 1). They are of two geomorphological types: "sand cays" are back reef sand deposits consolidated by beachrock (Tufaka, Fafa, Pangaimotu, Manima, Oneata, Malinoa, Monuafe, Onevai, Onevao, Motutapu, Fukave, Nuku, Ata and Tau), whereas "motus" are of raised limestone (Toketoke, Atata, Polo'a, Alakipeau, Velitoa Hihifo, Velitoa Hahake and Mokotu'u). The larger islands of the former type may have a raised limestone core around which sand and reef breccia have accumulated. Islands are mentioned in east-west order throughout this paper.

The islands result from the late Pleistocene and Holocene sea level history of the area. A narrow terrace at 7 m in the southern cliffs of Tongatapu was formed during the last interglacial (135±18 ka) (Taylor 1978). Since all raised limestone islands of the

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Tongatapu outliers are of 6 to 7 m in height, they would seem to be reef remnants fromthis highstand. The Holocene sea level record has included a stillstand 2.2 m higher than present, dated between 6500 and 5800 BP (Bourrouilh & Hoang 1976, Taylor & Bloom 1977). This mid-Holocene highstand was of regional extent, and the recent fall of sea level to present levels has been shown to promote sand islet formation (Schofield 1977). The sand cays of the Tongatapu islets are likely composed of dead reef material and scoured sand deposited on reef flats as sea level fell.

The climate of Tongatapu is tropical, with two seasonal divisions. The warmer wet season is from November to April, with warmest mean monthly temperature of 26.1°C in February (Thompson 1986). Two thirds of the 1900 mm mean annual rainfall falls during the wet season, which is also the cyclone season. The cooler dry season is from May to October, with coolest mean monthly temperature of 21.2°C in August, when droughts may occur periodically.

The south-east trades show remarkable constancy of direction, winds blowing from the eastern quadrant for 64.8% of the time (Thompson 1986). Cyclones during the
historic period show periodicity of 20 to 30 years (McLean *et al.* 1977, Oliver and Reardon 1982) with moderate to severe cyclones affecting Tongatapu 1874-1883, 1912-1913, 1930, 1964 and 1982. The most severe storm damage in recent years came with cyclone Isaac, tracking south-west through the Tonga group in early 1982 (Thompson 1986, Revell 1982). This affected Tongatapu most severely on the 2nd and 3rd of March, with winds moving from south-easterly, through easterly, then strongest winds from the north-east and north on the 3rd, with gusts up to 92 knots recorded. On Tongatapu, most low-lying northern areas were badly affected by floods from high seas and a heavy swell (Oliver & Reardon 1982, Woodroffe 1983). Variability in damage was a function of aspect, and degree of protection within the central lagoon and behind reefs.

Ocean tides at Nuku'alofa are semi-diurnal with a slight diurnal inequality. The mean tidal range is 1.07 m, and the spring range is 1.22 m (US National Oceanic and Atmospheric Administration 1986).

The terrestrial flora of Tongatapu comprises 340 vascular plants (Arthur Whistler, pers. comm.). The natural vegetation of inland Tongatapu has been cleared for *Cocos* plantations and intensive small-holder agriculture (Thaman 1975), except for a small forest near Fua'amotu airport. Mangrove forests fringe the north shore and the central Fanga 'Uta lagoon, and natural coastal forest fringes the rugged south coast, and occurs on the northern islets.The vegetation of four sand cays nearest to Tongatapu: Pangaimotu, Makaha'a, Manima and Oneata was mapped by Stoddart in 1969 (Stoddart 1975). Following Cyclone Isaac in 1982, Woodroffe mapped these as well as Tufaka, Fafa, Monuafe and Malinoa (Woodroffe 1983).

Tongatapu is the most populated island in the Kingdom of Tonga, with 61 000 in the 1976 census, most living around the capital, Nuku'alofa. The terrestrial ecosystems of all outlier islands have been disturbed as a result of human influence. The intensity of human impact can be categorised on the basis of visitor frequency or size of the resident population.

1) Islands with many visitors a day include Atata, Fafa and Pangaimotu, with tourist resort developments; Manima and Oneata, which can be walked to easily at low tide; and Ata, which is a low security prison camp.
2) Islands with several visitors a week are those with a resident family, comprising Onevai, Velitoa Hahake and Fukave. Motutapu, periodically used for training by the Tonga Defence Force (TDF) is also included, as is Velitoa Hihifo, which is used as a TDF store, and looked after by the family on Velitoa Hahake.
3) Islands with several visitors a month are those used for cultivation, or popular stopping places on fishing or recreational boat trips. These include Polo'a, Alakipeau, Makaha'a and Nuku.
4) Islands with infrequent visitors may have low intensity agricultural use, and tend to be smaller and/or further away from Tongatapu. These include Toketoke, Tufaka, Monuafe, Malinoa, Mokotu'u, Onevao and Tau.

Examination of the combined effects of alternative geomorphological types, varied area, isolation and degree of human disturbance on the distribution of members of a relatively large pool of terrestrial plant species forms the basis for this study.

Methods

Islands were visited between May 1987 and January 1988, and on all except the larger island Atata, a total species count was made of vascular plants. Morphological features and vegetation units were mapped for those islands not covered by Woodroffe (1983), and area determined.

It is possible to walk to Pangaimotu (approaching from the east), Manima and Oneata, with sand flats between being quite dry at low tide. Polo'a and Alakipeau can be reached by horse, or a wet walk, along a path through seagrass from Muifonua Point. All other islands must be reached by boat, with a frequent tourist boat service to Atata, Fafa and Pangaimotu.

Morphological features and vegetation units were mapped on Toketoke, Polo'a, Alakipeau, Velitoa Hihifo, Velitoa Hahake, Onevai, Onevao, Motutapu, Fukave, Nuku, Ata and Tau (Figures 2 to 13), these islands not being mapped previously. On smaller islands (Toketoke, Alakipeau, Velitoa Hihifo and Tau), this was by tape-and-compass, with a central line and perpendicular offsets to each coast every 25 m, and by pace-and-compass on larger islands, with systematic transects run inland from the coast. Maps of other islands from 1982 are given by Woodroffe (1983).

Area was determined by laying a transparent grid over these maps, and counting square mm. Island areas given in Table 7 are defined by limit of vegetation, not high tide mark. Future researchers should note that the area figures available from the Ministry of Lands and Surveys are rounded to the nearest acre, and are of variable accuracy.

Physiognomic types identified in mapping were coastal trees, shrubs, herbs, coconut woodland and mangroves, though sections dominated by a particular species are identified separately. Most units were diverse, a function of the relatively large flora of Tongatapu. Species present were noted or collected during surveying, hence larger

islands were less intensively covered than smaller. Suggested error margins for species missed on the total species figures (Table 7) are +1 on small islands and +5 on larger islands .

Species names and physiognomic classifications are largely taken from Yuncker (1959), Smith (1979-81), and Whistler (1983), also a number of experts assisted in identifying species, acknowledged below. Use was also made of Yuncker's herbarium collection, held at the Ministry of Agriculture, Forestry and Fisheries Research Farm at Vaini.

Vegetation units

An inventory of the species of trees, shrubs, herbs, vines, grasses and sedges, and ferns on each island is presented in Tables 1 to 6. Island areas and species totals are given in Table 7. A total of 203 vascular plants were identified, inclusive of weeds and cultivated plants. The vegetation units shown in Figures 2 to 13 are described below.

COASTAL TREES

The composition of coastal tree units varied from west to east across the island group, with shelter provided by Tongatapu from the prevailing south-east trades increasing westwards. Maria Bay is sheltered behind the reef to the east of Polo'a and Atata (Figure 1), causing western shorelines of Polo'a, Alakipeau and the southern spit of Atata to be dominated by Vitex, in association with Thespesia, Cerbera and Hibiscus.

Coastal thickets dominated by Hibiscus occurred on islands central to the group, on Pangaimotu, Makaha'a, Manima and Oneata, as shown in Woodroffe's (1983) maps. Beach thickets were in association with Thespesia, Hernandia and Cordia. On the raised limestone islands of Toketoke, Northern Atata, and parts of Alakipeau and Velitoa Hihifo, particularly dense Hibiscus stands occur.

In more exposed, windward locations, Acacia, Pandanus, Tournefortia (=Messerschmidia), Pisonia and Phaleria, Terminalia and Leucaena become dominant. The maps of Toketoke, Polo'a and Alakipeau show Pandanus stands on the edges of east facing overhanging rock, and Table 1 in listing islands from west to east clearly shows increased occurrence of these species towards the east. Casuarina also showed greater frequency towards the east, but only on rocky outcrops. Tournefortia and Pandanus frequently occurred opportunistically within shrub and herb units, as shown in Plate 1.

Certain islands were unusually dominated by one species in particular, showing that competitors were absent or poorly established. Examples were Leucaena on Tufaka and Monuafe, Neisosperma on Fafa, Syzygium richii on Motutapu and Pisonia on Fukave and Nuku. Motutapu featured an unusually diverse and well established coastal forest, presumably due to conservation by TDF ownership.

COASTAL SHRUBS

Frequent components of the coastal shrub unit were Scaevola, Colubrina, Wollastonia (=Wedelia) and Jasminum didymum on all islands, also Clerodendrum more commonly on western islands, and Suriana more commonly on eastern islands. Wollastonia was most frequent on the edges of raised limestone cliffs, and Scaevola opportunistic of sand areas recently colonised by vines and herbs, such as the south point of Malinoa.

HERBS

Most of the 52 herbs listed in Table 3 are weed species inadvertently introduced by man. Hence the islands identified as most frequently visited have floras significantly increased by these weeds (Pangaimotu, Manima, Oneata and Ata), while those uncommonly visited have very few or none (Toketoke, Tufaka, Malinoa, Mokotu'u and Tau).

The weeds Rivina, Stachytarpheta and Lantana are most successfully established, commonly on untended cultivated areas under Cocos. Rivina forms extensive stands across central areas of Fukave, Stachytarpheta being absent, as shown in Plate 2.

Bidens, Emilia, Euphorbia hirta, and Malvastrum are also common. These weeds are most successful in open areas under Cocos, forming a lawn-like cover around buildings, such as around the resorts on Fafa and Pangaimotu, also the west of Velitoa Hihifo and Motutapu, and the east of Fukave and Ata.

Goats on Motutapu and pigs on Makaha'a disrupt the herb layer by rooting and grazing, causing fewer herbs to be present on these islands.

Of the native coastal herbs, Sesuvium is most common, occupying large expanses within the mangrove area of the centre of Onevai, also colonising offshore rocks and upper portions of beachrock on other islands.

On the more extensive beaches of Malinoa and Tau in particular, areas of loose beach sand are colonised by the vines Canavalia, Vigna and Ipomoea pes-caprae, and the grass Thuarea, as shown in Plate 3. Euphorbia atoto is also a successful coloniser of loose sand, seeming to be a native element of the flora.

MANGROVES

The largest mangrove area on the Tongatapu outliers is the central area of sand flats on Onevai, now open to tidal influence from the south, though the chart by Aldrich (1888) shows this area to open to the west. Patch stands of Rhizophora stylosa are most extensive, though Bruguiera gymnorrhiza and Rhizophora mangle (=R. samoensis) also occur. Slightly higher intertidal sands are covered by Sesuvium.

Rhizophora occurs on sheltered shorelines of other islands, but merely as isolated individuals, offshore of the northwest point of Pangaimotu, as photographed by Stoddart (1975), and on beachrock to the west of Polo'a and Alakipeau. R. stylosa is more common than R. mangle in these locations, showing the preference of the latter for more brackish waters (Chapman 1970).

Excoecaria is a mangrove species, but occurs on most islands as individual trees in beach habitats.

COCOS WOODLAND

On most islands, Cocos woodland occurred inland, and many examples of planting were seen. The east of Tau was cleared and planted with Cocos in 1985, and Woodroffe (1983) described young Cocos palms to 7 m on Monuafe, which were absent in 1987. Planted lines are particularly apparent on Fafa and Pangaimotu. Headless stumps from the 1982 cyclone still remained on Toketoke and Tufaka. On Onevao and Makaha'a, Cocos occurs to the edge as these islands are badly eroding, with loose soil cliffs to 2 m in height on all sides.

Cocos occurs in emergent association with coastal trees such as Calophyllum, Neisosperma, Barringtonia, Cerbera, and Hibiscus. Planted species such as Carica, Morinda and Artocarpus are also common, as well as the weed-like Psidium. More disturbed units under Cocos are sub-classified on the maps as "Cocos over herbs and low weeds", including both the lawn-like cover described above and recently cleared areas on Tau; "Cocos over shrubs and scrub" is a less tended version of this, and where the palms rise above a ground cover of tall Panicum maximum, "Cocos over grass" is used.

GRASS

Areas of open grass occurred only on raised limestone islands, of tall clumps of Panicum (up to two meters high) interdispersed by occasional weeds, vines and shrubs. Large areas occurred on Toketoke and Velitoa Hihifo, and could be resultant from neglect after clearance of Hibiscus thicket.

The shooting range on Motutapu is also mapped as grass, but this is a closely mown open lawn.

Fauna

Three islands had large bird populations: the reef heron (Egretta s.sacra) on Toketoke, and the common noddy (Anous stolidus) on Fukave and Nuku. The latter were in association with the large Pisonia stands. Identification was from Watling (1982).

The flora of Mokotu'u is an interesting reflection on transportation of seeds by birds. This is a limestone outcrop to the NW of Onevai, 10 m in diameter and about 6 m high, undercut on all sides. Drift seeds could not reach it, and though I heard

accounts of people climbing onto it, this would be extremely rare. Hence the species present must result from seed dispersal by birds.

Discussion of floristics

A log area/ number of vascular species plot for the Tongatapu outliers is given in Figure 14, showing that there is an approximately linear relationship as described by Preston (1962) and MacArthur and Wilson (1967). The scatter of data around this trend can be explained by several factors.

Sand cays and motus are distinguished on the graph, clearly showing that at all island sizes, raised limestone islands are more diverse than sand cays. Two factors seem to be of importance, degree of storm disturbance, and habitat heterogeneity. Woodroffe (1983) noted that raised reefal limestone coasts underwent little morphological change during Cyclone Isaac, while greatest changes were observed on sand islands. Hence, referring to MacArthur & Wilson's (1963) equilibrium model, where species number is a result of balanced immigration and extinction rates, the extinction rate resulting from storms will be higher on a sand cay than a motu of the same area. Protection is given by the irregular and immobile rock surface, that also provides a diversity of microhabitats between hollows and outcrops, as well as a surface area that exceeds the spatial area of the island. By comparison, sand cays are uniform in microclimate and micromorphology. This refinement of the MacArthur & Wilson (1967) species/ area model of island biogeography on the basis of habitat diversity was made by Sauer (1969) and Buckley (1982), the latter finding similar variance in diversity of flora on sand and limestone islands in the Lowendal archipelago, Western Australia.

Floristics of the islands is also shown to be influenced by the degree of human disturbance, on four recognisable scales as described. Chaloupka & Domm (1986) found on 10 cays of the Southern Great Barrier Reef that percentage of alien plant species recorded on a cay is positively related to the frequency of human visitor traffic to that cay, independent of cay size. On the Tongatapu outliers, it would seem that resources on islands larger than 8 ha. cause them to be inhabited regardless of location, while all islands under 4 ha. are uninhabited, with the exception of Velitoa Hahake. In Figure 14, the sand cays show greatest vertical scatter of data within these area thresholds, some being frequently visited and therefore having larger floras with weeds and cultigens, while others are of a similar area and yet relatively undisturbed.

Within this marginal range of 4 to 8 ha., degree of human influence and consequent species number is a function of distance from Tongatapu. Oneata is permanently inhabited, Motutapu intermittently inhabited, and Nuku deserted to leave decaying buildings. As stated earlier, habitation of Velitoa Hahake is an unusual case, resulting in lack of normal vegetation units and a disturbed appearance. In this context, MacArthur & Wilsons' (1967) proposition that isolation results in a low species number on islands would be true. In the more traditional application, the more distant islands of the group, Malinoa and Tau, occur below the best fit line in Figure 14, but are not significantly more depauperate in flora relative to other sand cays with a similar level of human visitation further south.

Data from other island groups also show greatest range in number of species on islands of 4 to 8 ha., from the Belize sand cays (Stoddart & Fosberg 1982: 531) and Kapingamarangi Atoll (Niering 1963: 137), suggesting that within this range there is variable human influence. This could be due to distance from population centres as shown for Tongatapu, or some other factor of convenience for human use, such as persisting dense thicket, or swampy areas.

Variation in floristic composition of the Tongatapu outliers that is related to island position has been described, all islands east of Motutapu being exposed to prevailing winds, while those to the west are in the lee of Tongatapu. This causes greater frequency of certain plants to the west or east according to their ecological preferences, and on a smaller scale, similar patterns are visible in comparison of west and east coasts of each island.

The Tongatapu outliers data do not show a constant number of species on all islands of less than 1.4 ha. as identified by Wiens (1962) and Whitehead and Jones (1969). Rather, species number of these smaller islands is quite varied, owing to differences in substrate type and frequency of human visitation. However, the flora of small sand islands such as Tufaka and Monuafe did seem to be less well established than larger islands, with many species comprising the counts being just one individual germinated on the upper beach.

Conclusion

Relative to other locations where species/ area studies have been carried out, the Tongatapu outliers have a large local flora owing to the size of Tongatapu, causing an overall greater species density on all islands. This provides a useful data set for comment on the factors controlling floristics of the group. Raised limestone islands are shown to be more diverse than sand cays, reflecting habitat diversity and substrate stability. Floristic composition varies from east to west across the group, from windward to leeward conditions. A threshold of 4 to 8 ha. of uncertainty between no and certain anthropochory is identified, within which degree of human use and consequent floristic changes are a function of convenient use of the marginal island, with distance from the mainland being the most important controlling factor here. These factors cause variation within a basic trend for number of species to be related to island area.

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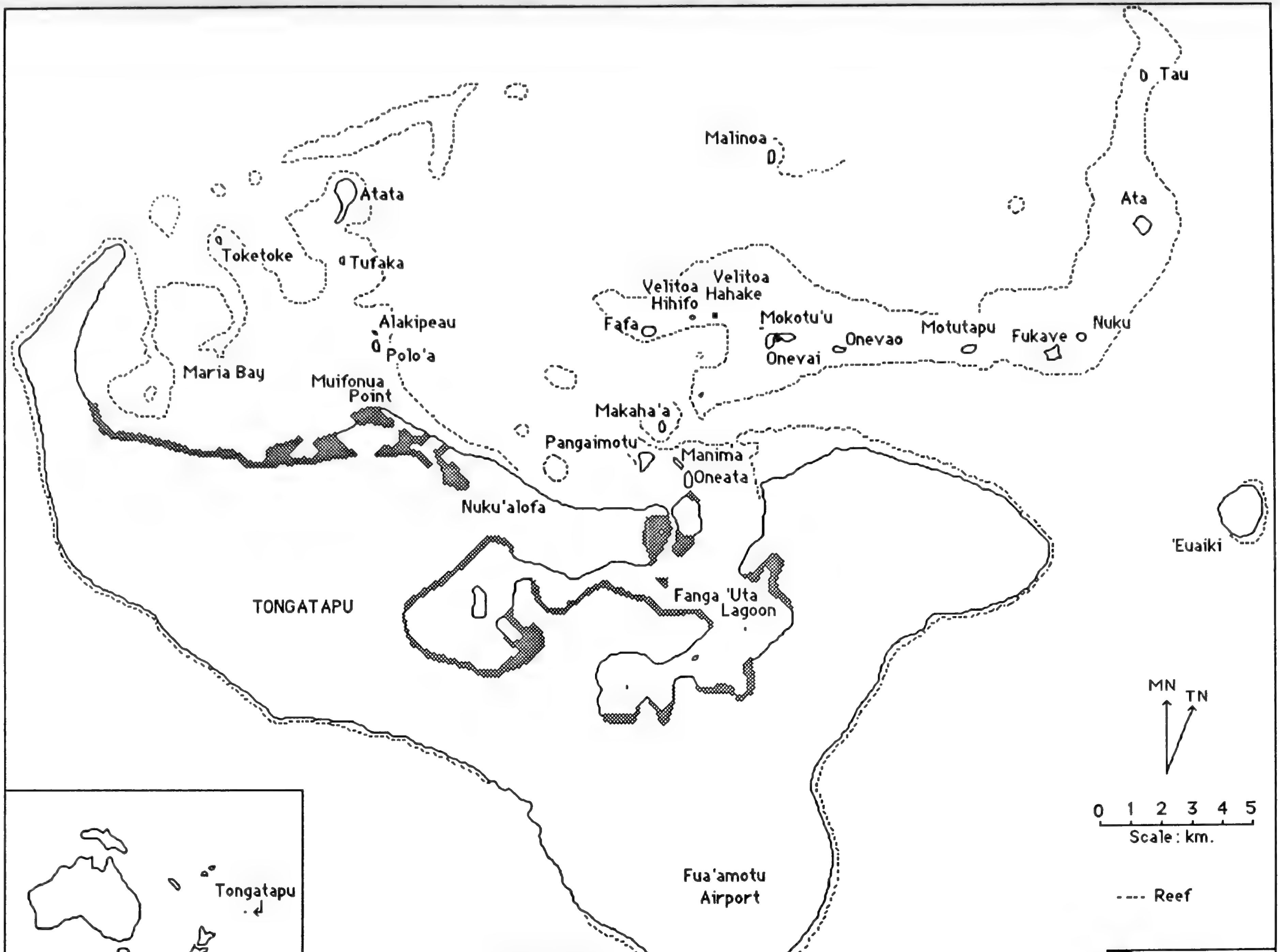


Figure 1 : The Tongatapu Outliers

Key to Figures 2 to 13

Herbs and low weeds
Shrubs and scrub
Coastal trees
Hibiscus thicket
Cocos woodland
Cocos over grass
Cocos over shrubs and scrub
Cocos over herbs and low weeds
Grass
Mangrove

Pandanus
Casuarina
Pisonia
E Excoecaria
C Calophyllum
c Cerbera
P Pittosporum
T Tournefortia
H Hernandia

Beachrock
Sand
Raised limestone cliff
Building
Fence
--- Path

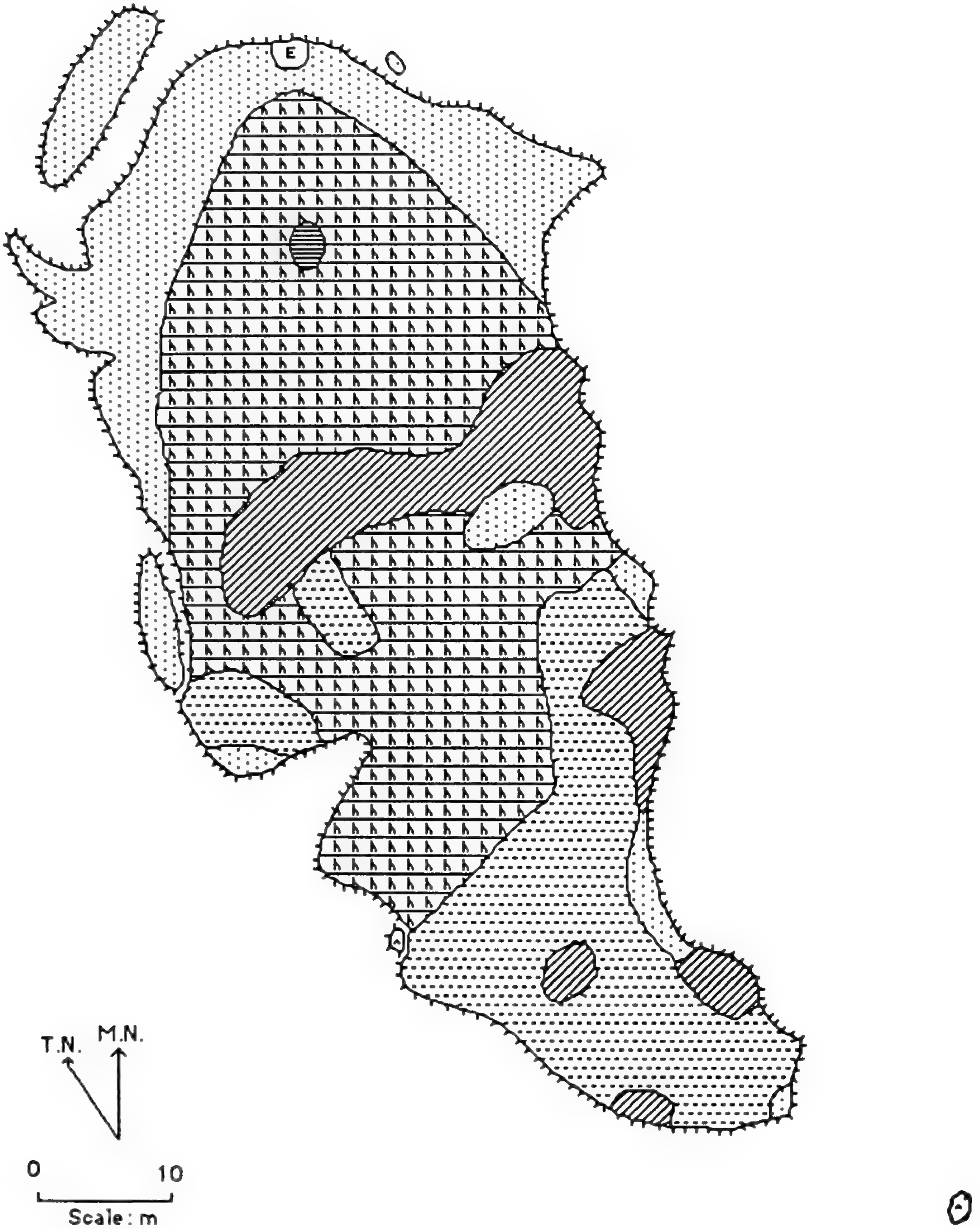


Figure 2: Toketoke

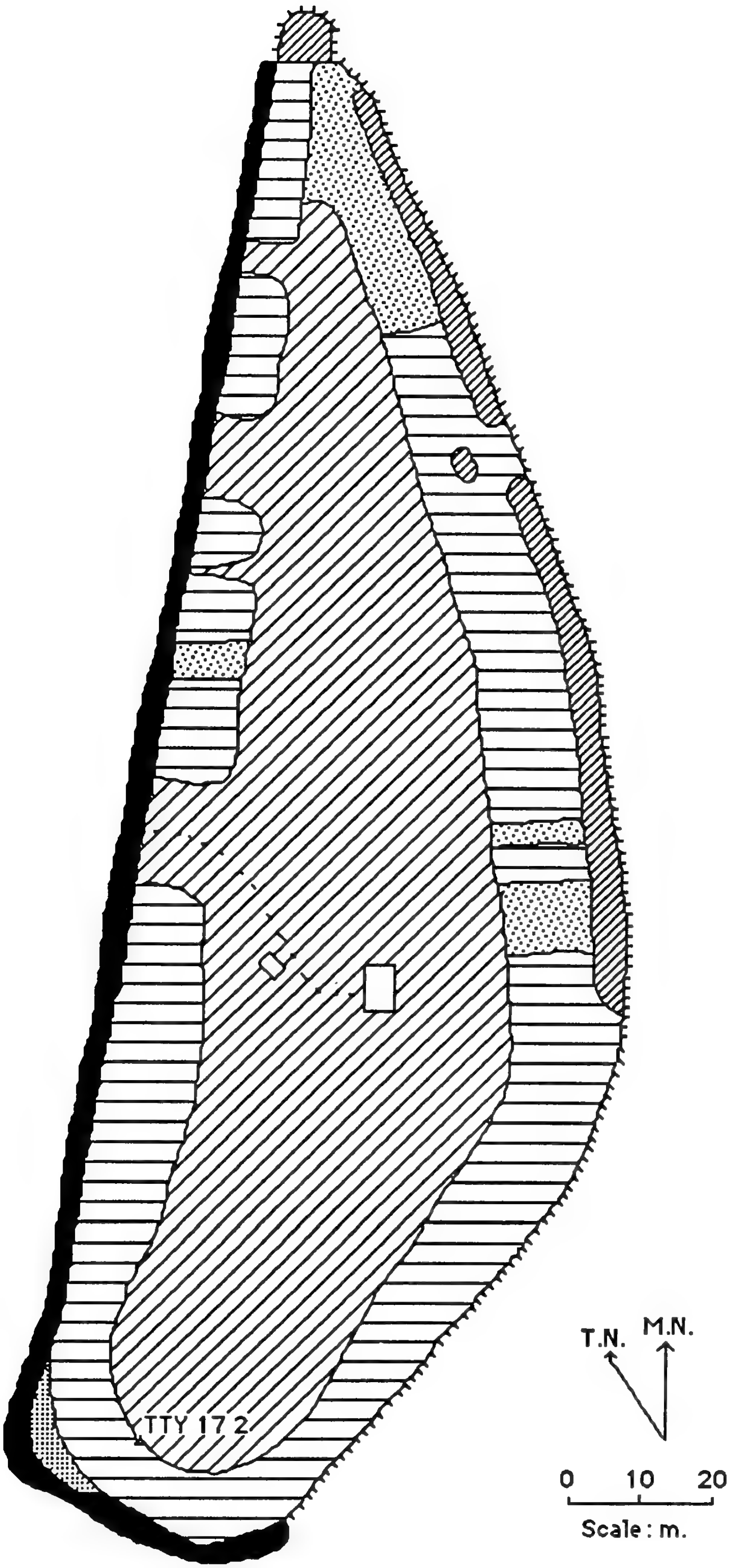


Figure 3: Polo'a

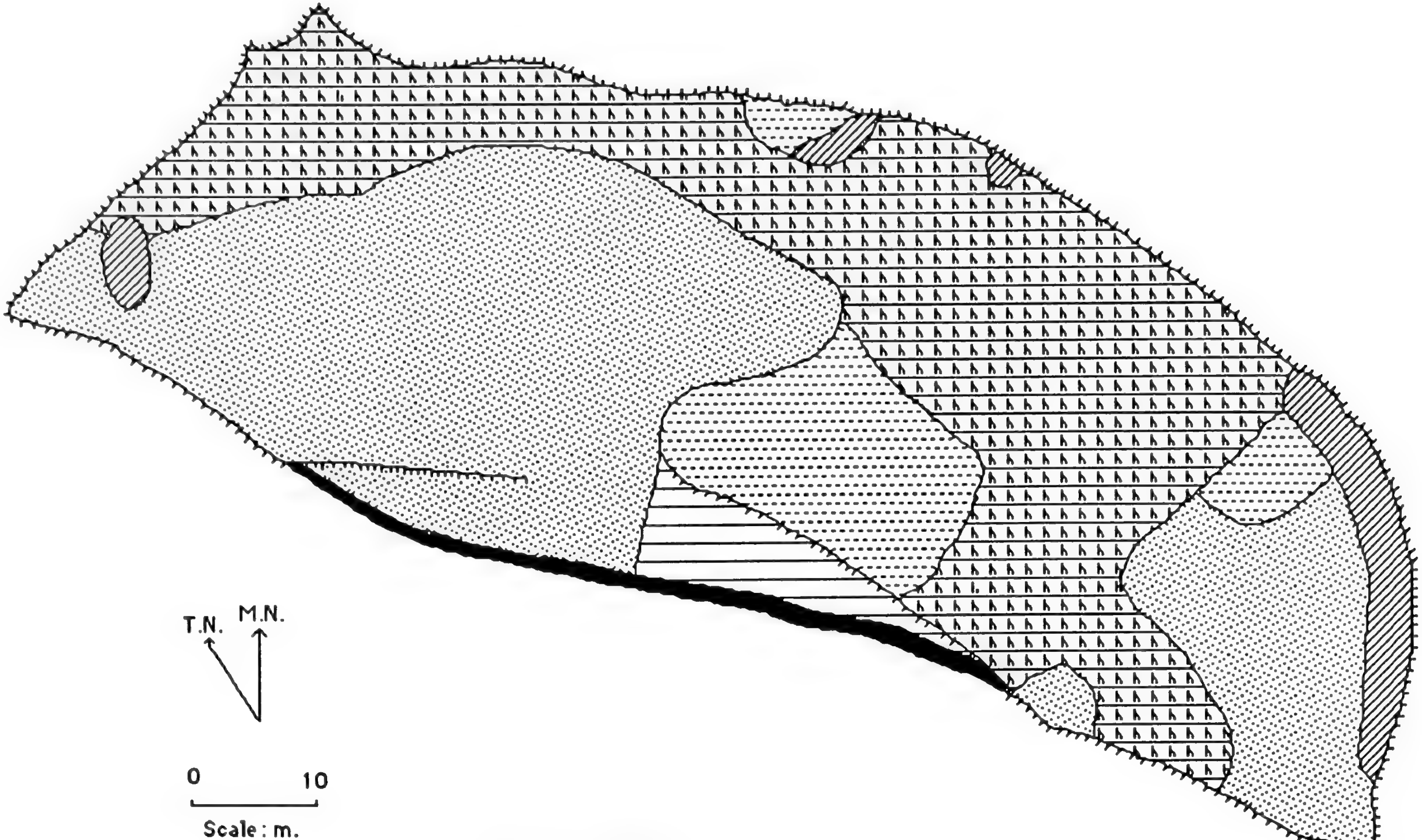


Figure 4: Alakipeau

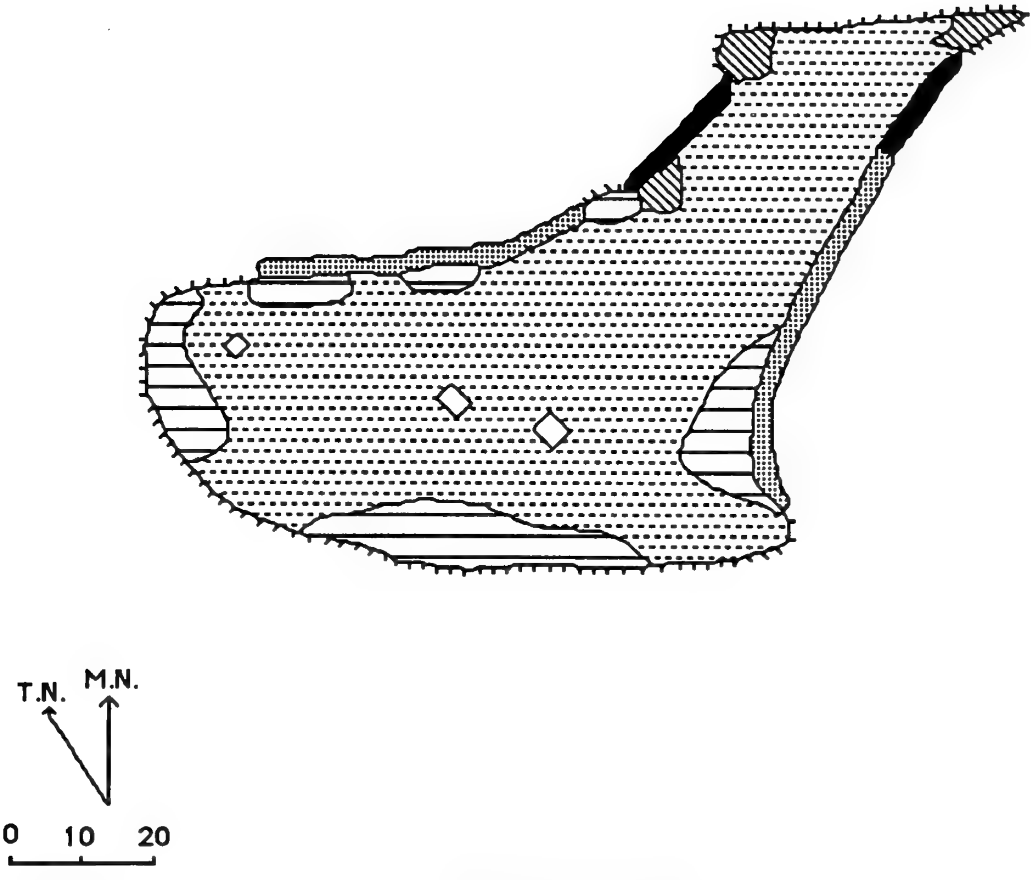


Figure 5 : Velitoa Hihifo

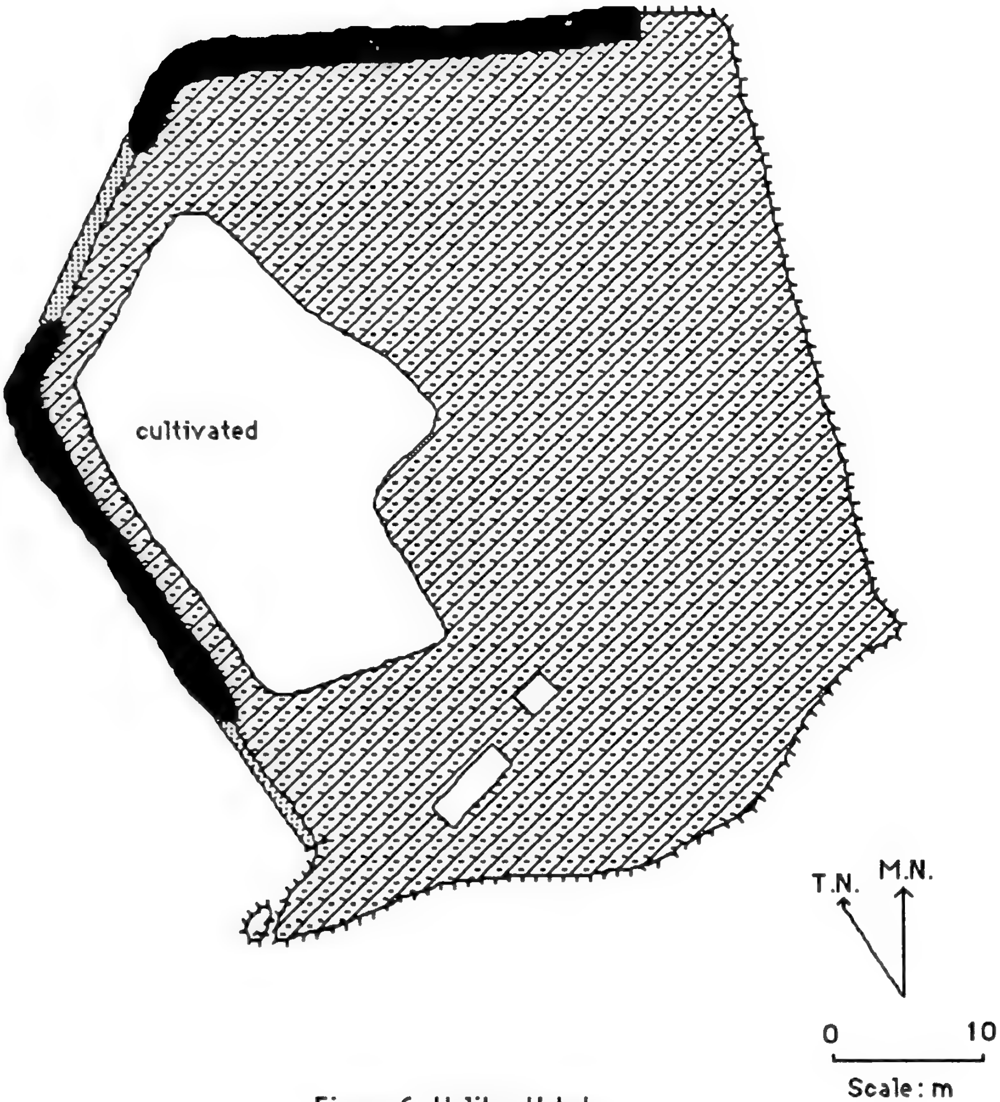


Figure 6 : Velitoa Hahake

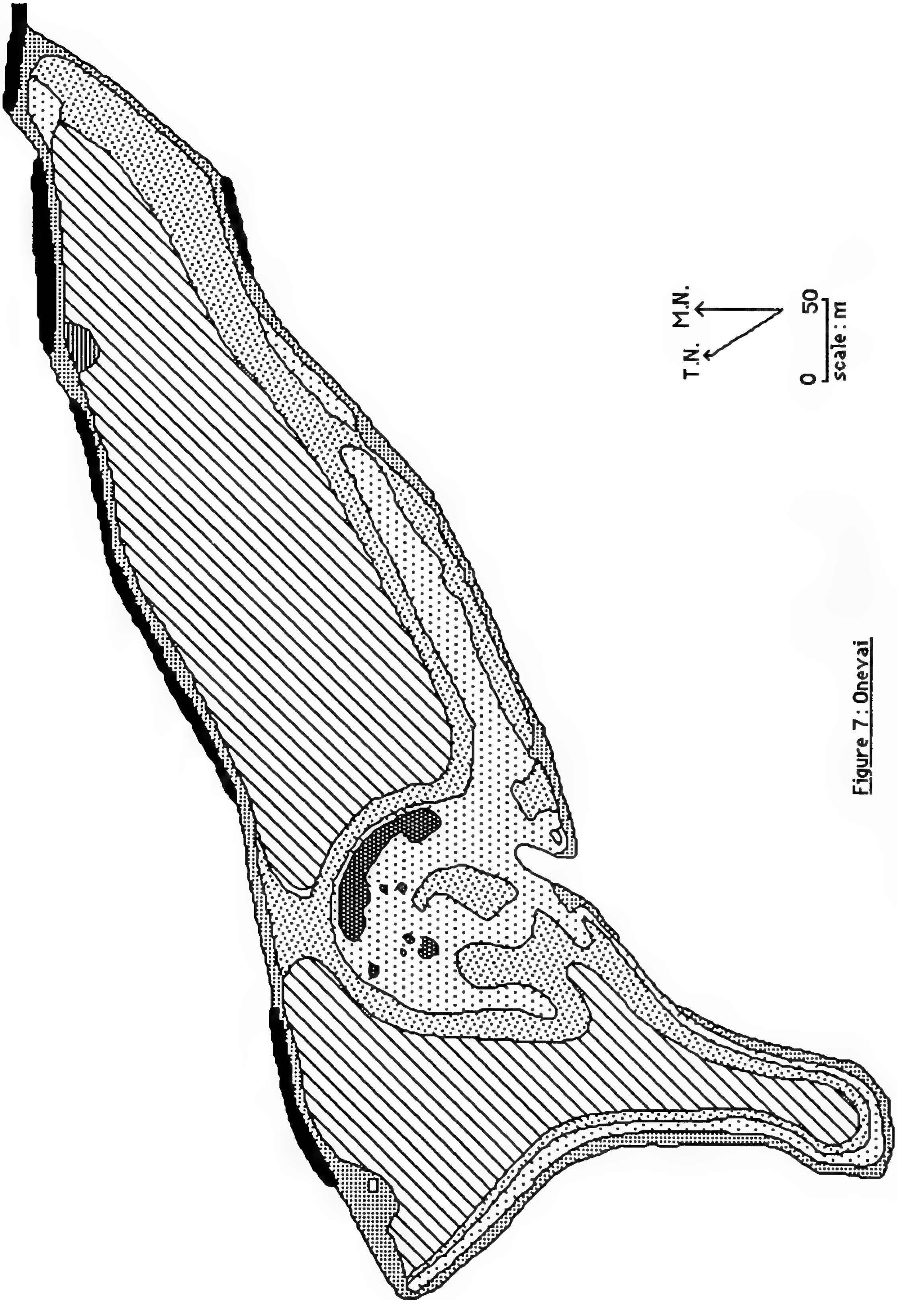


Figure 7: Oneyai

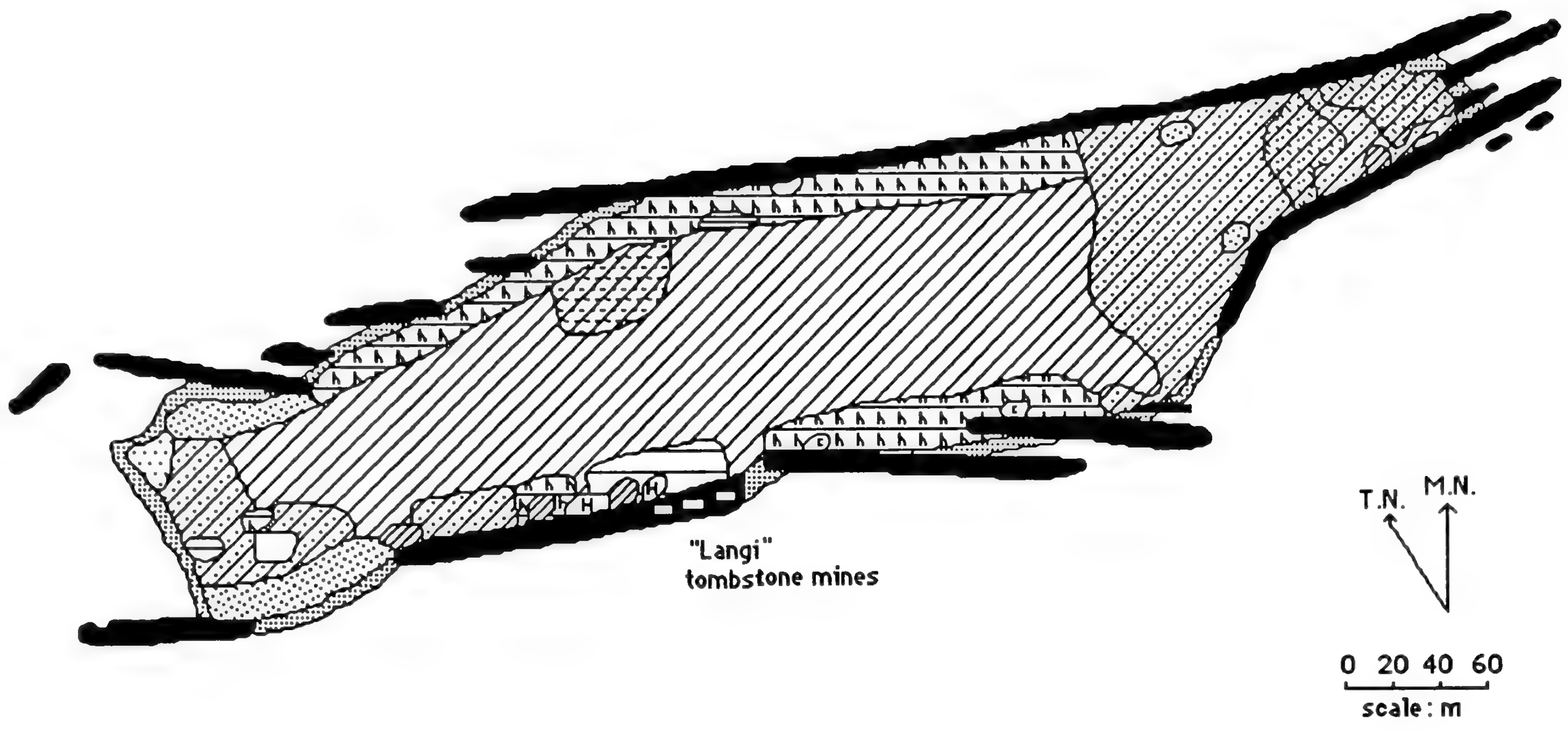
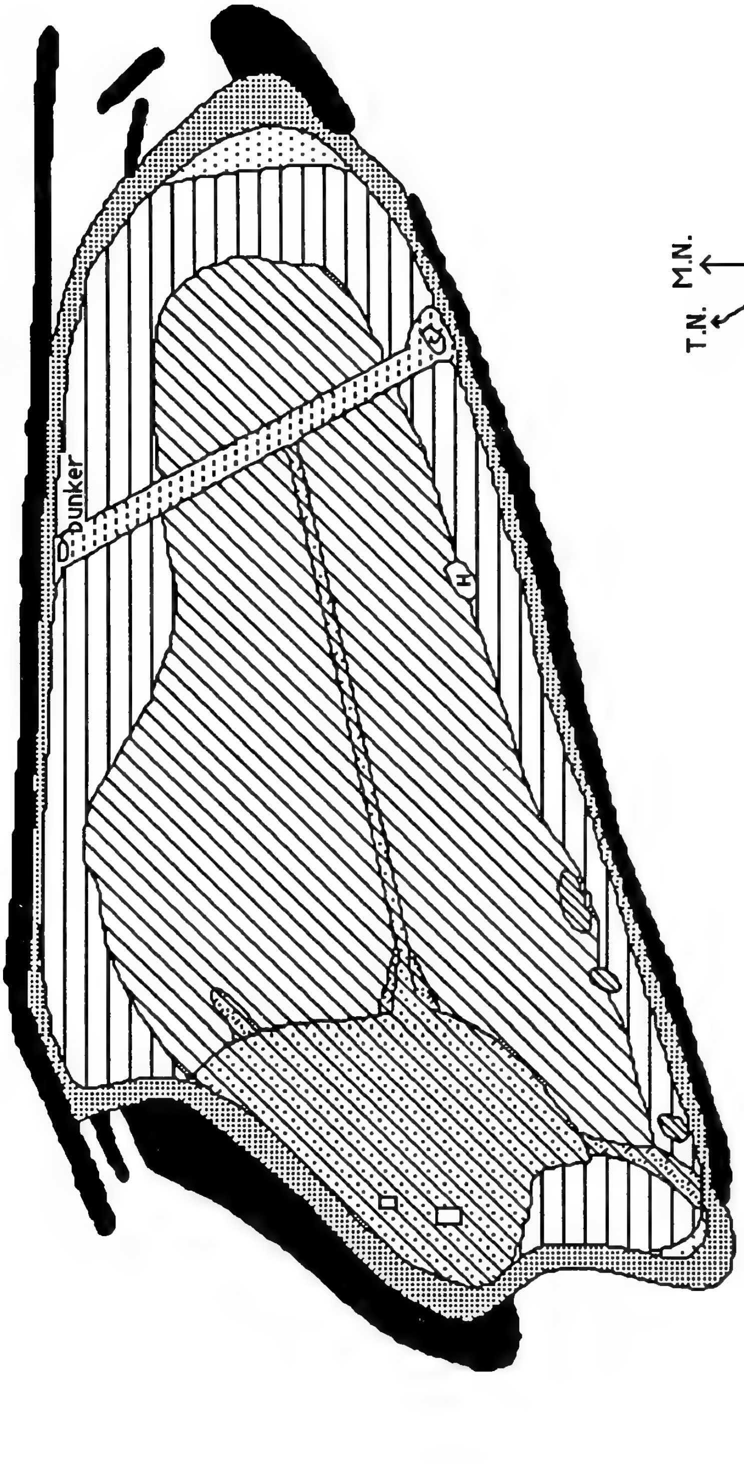


Figure 8 : Onevao



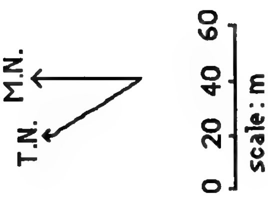


Figure 9: Motutapu

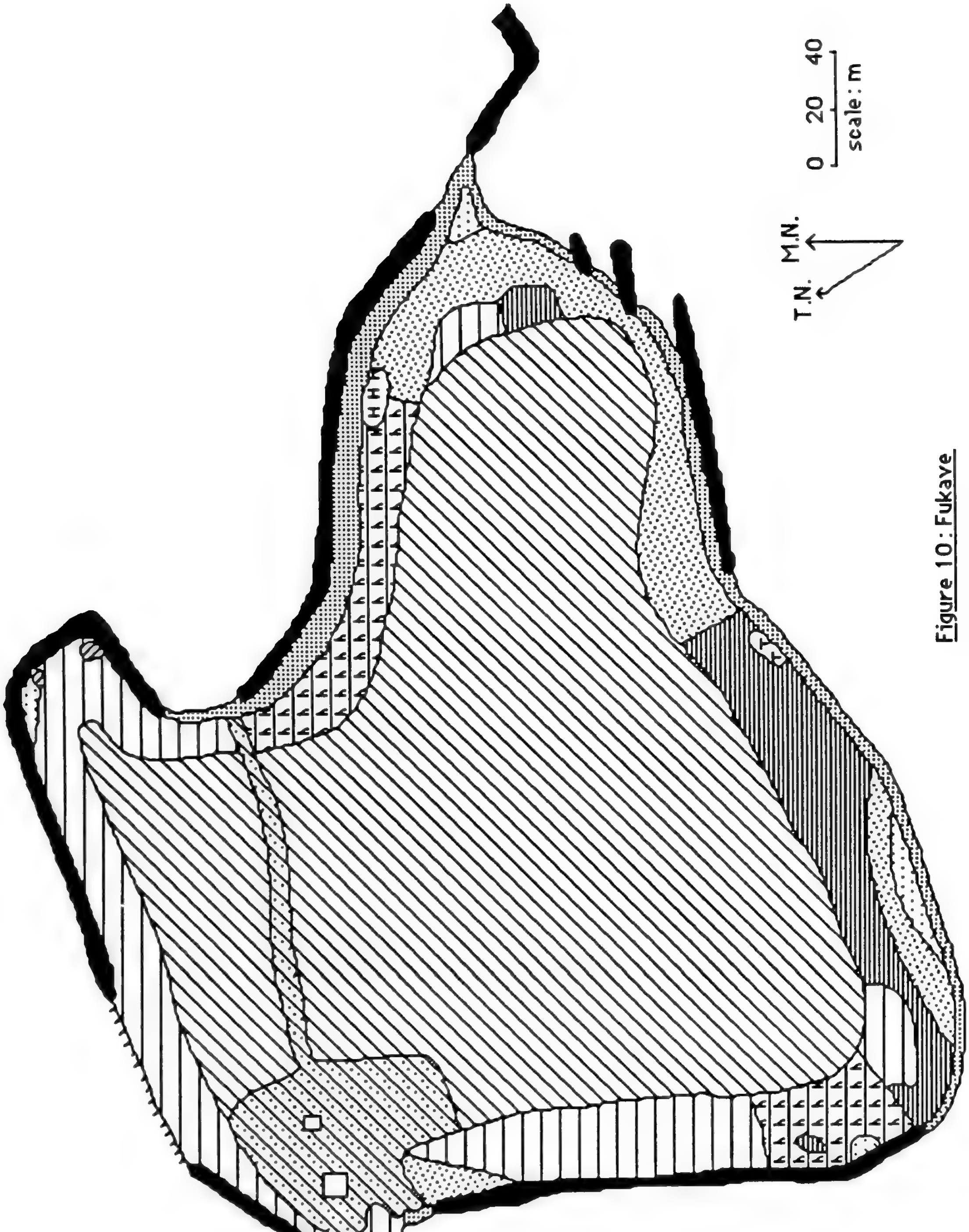


Figure 10 : Fukave

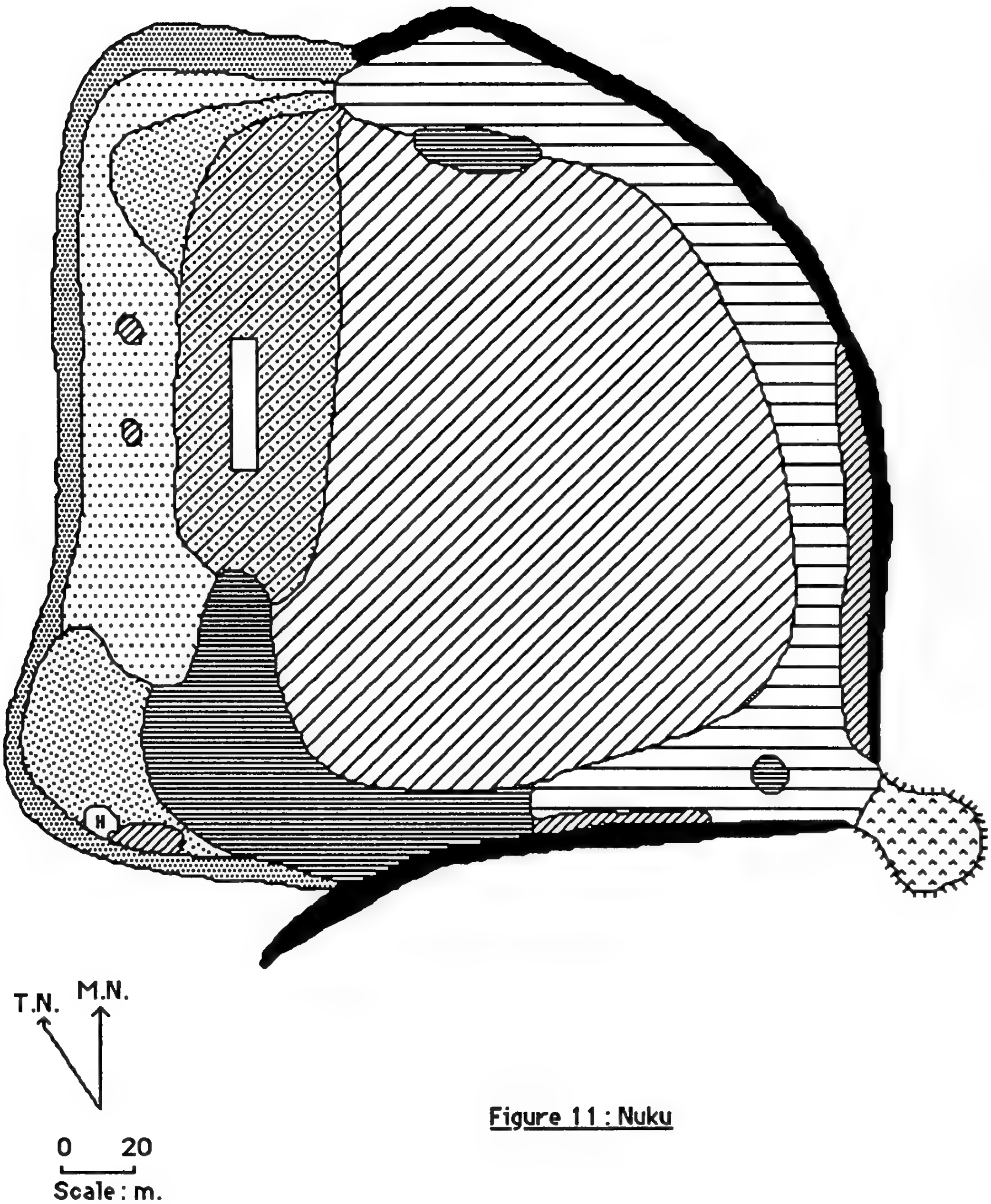


Figure 11 : Nuku

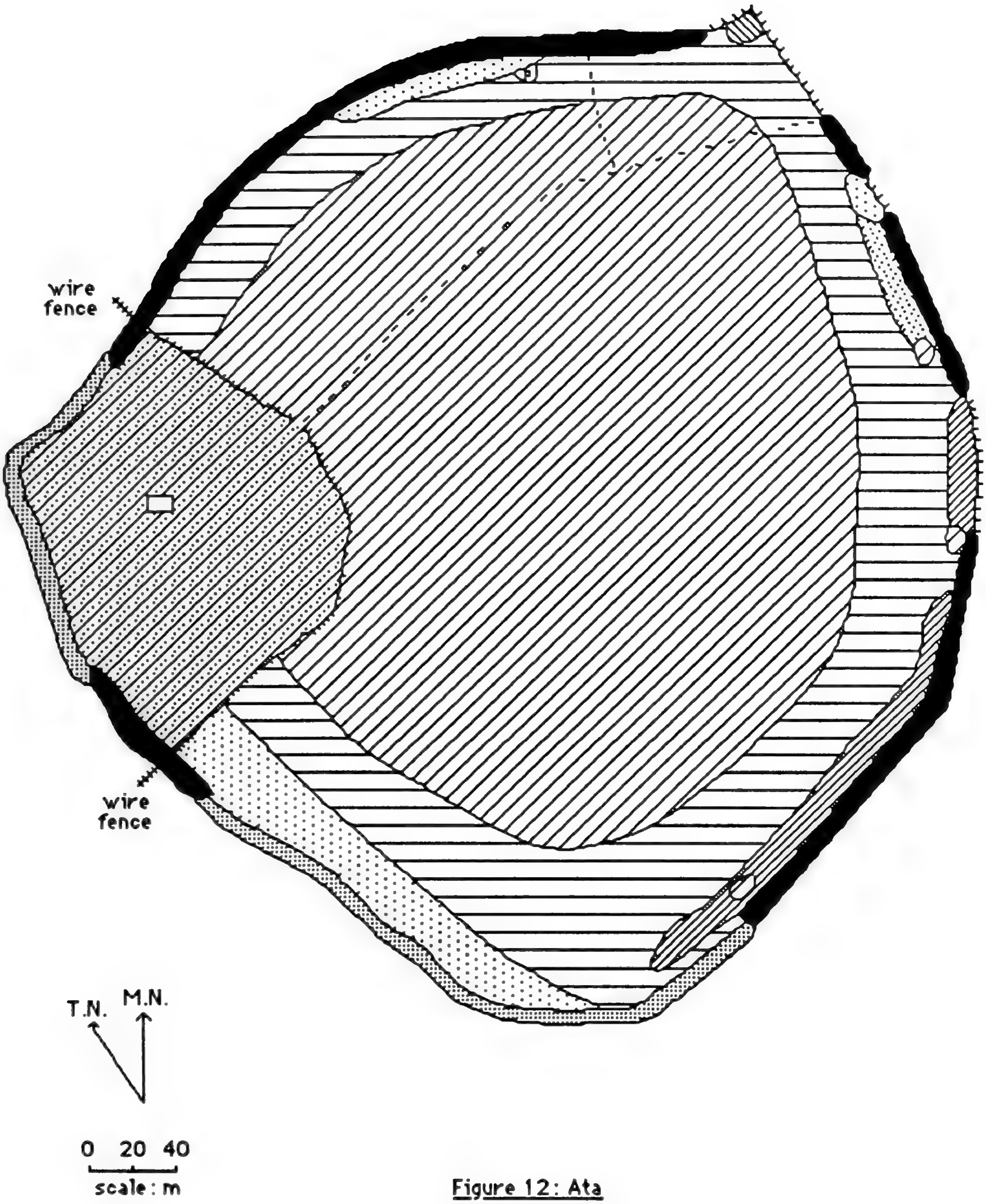


Figure 12: Ata

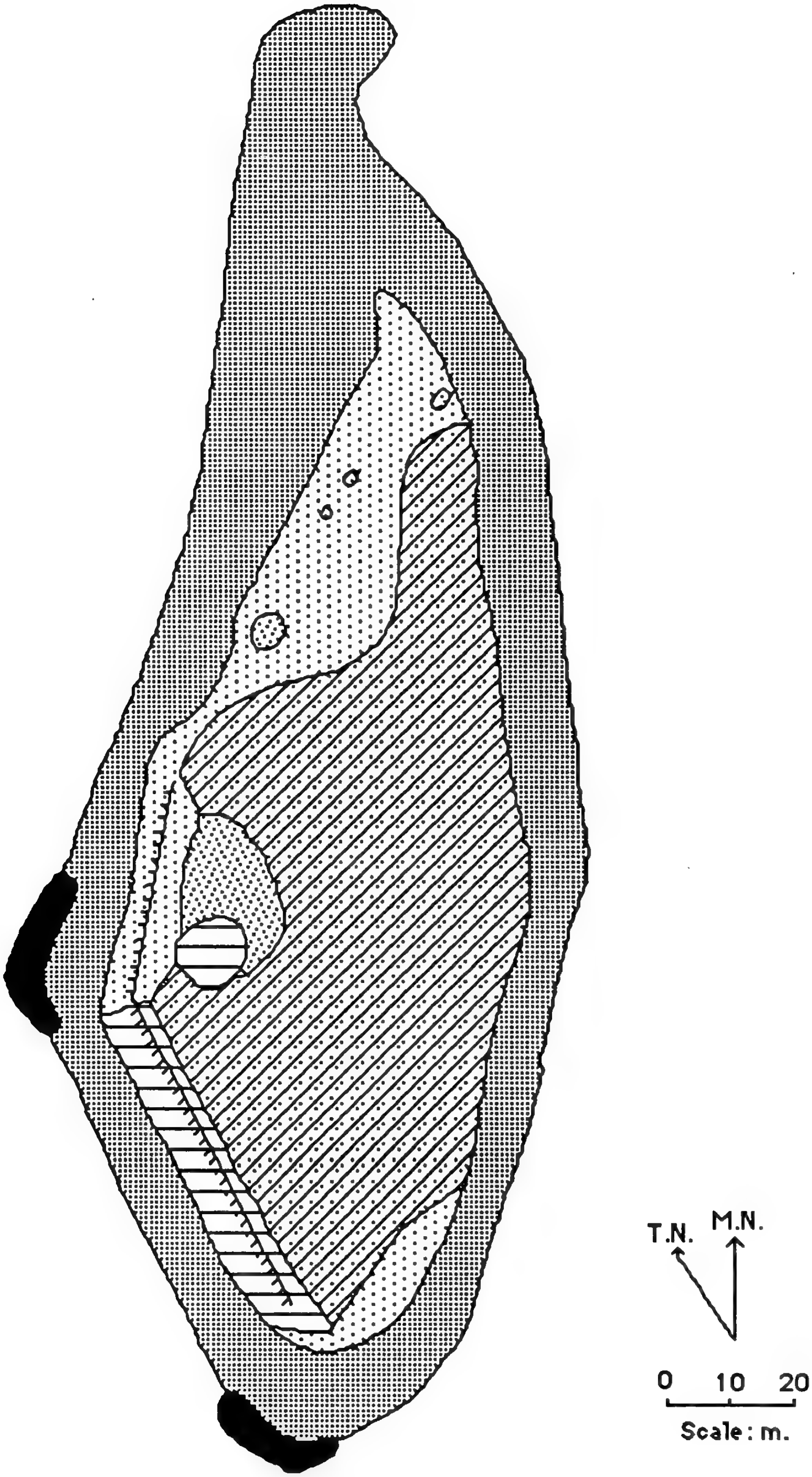


Figure 13: Tau

Figure 14 Number of species/ area plot for the Tongatapu outliers

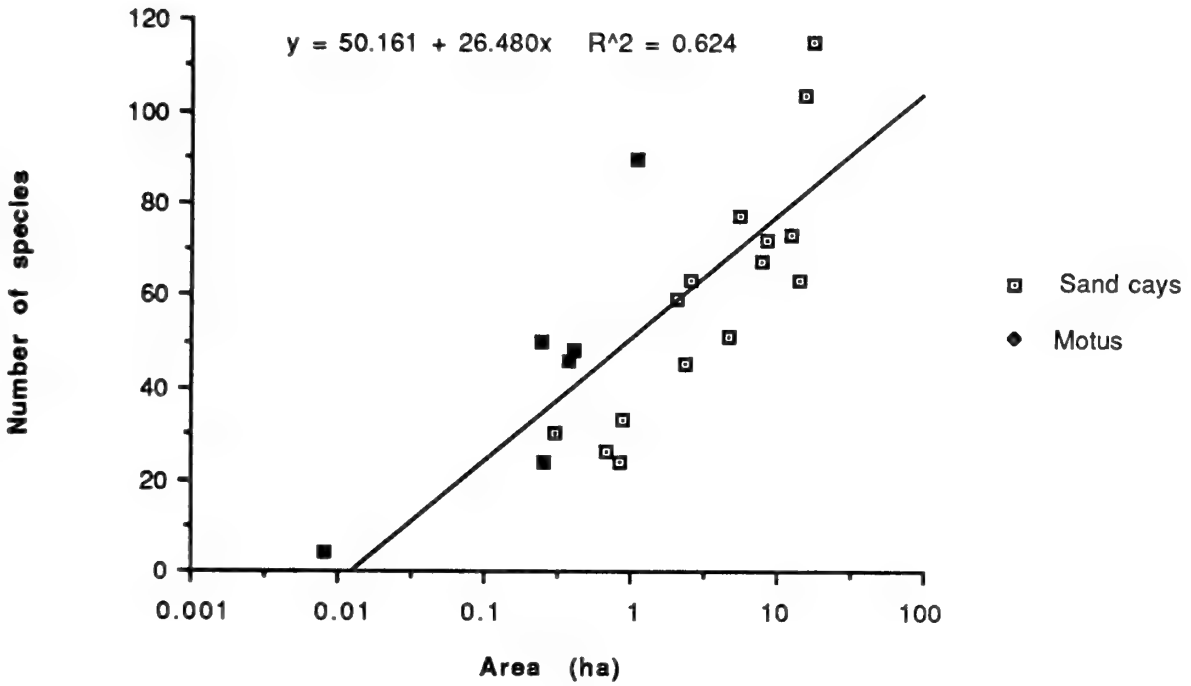


Table 1A. Distribution of tree species on the Tongatapu outliers

	Toketoke	Tufaka	Polo'a	Alakipeau	Fafa	Makaha'a	Pangaimotu	Manima	Oneata	Malinoa	Monuafe	Velitoa Hihifo	Velitoa Hahake	Mokotu'u	Onevai	Onevao	Motutapu	Fukave	Nuku	Ata	Tau
Acacia simplex		X			X	X	X	X	X	X	X				X	X	X	X	X	X	X
Aleurites moluccana			X						X									X			
Alphitonia zizyphoides					X				X												
Annona reticulata			X																		
Artocarpus altilis						X	X		X								X	X		X	
Barringtonia asiatica			X	X			X			X			X				X			X	
Bruguiera gymnorrhiza															X						
Bischofia javanica							X														
Calophyllum inophyllum					X	X	X	X	X	X	X				X	X	X	X		X	X
Carica papaya	X		X		X	X	X	X	X			X	X		X	X		X	X	X	
Casuarina equisetifolia			X		X	X	X		X			X		X	X			X		X	
Canthium barbatum																					
Cerbera odollam			X	X	X	X	X	X	X	X	X		X			X	X			X	
Citrus maxima	X			X		X	X					X	X			X				X	
Cocos nucifera	X		X	X	X	X	X	X	X	X		X	X		X	X	X	X	X	X	X
Cordia subcordata			X			X	X	X	X	X	X				X						
Cycas rumphii						X							X					X		X	
Diospyros elliptica			X		X		X	X	X						X		X	X		X	
Dysoxylem forsteri			X		X												X				
Elattostachys falcata						X									X						
Erythrina fusca						X										X	X				
Eucalyptus sp.							X														
Euphorbia tirucalli							X								X						
Excoecaria agallocha			X	X	X	X	X	X	X		X		X		X	X	X	X	X	X	
Ficus obliqua																		X			
Ficus scabra							X														
Ficus tinctoria			X													X	X			X	
Garcinia pseudoguttifera			X																		
Geniostoma vitiense															X		X				
Glochidion concolor			X				X		X								X				
Grewia crenata	X				X		X	X	X						X	X				X	X
Guettarda speciosa					X	X	X		X	X					X		X	X	X		
Heritiera littoralis			X	X			X														
Hernandia nymphaeifolia					X	X	X	X	X	X					X	X		X	X	X	X
Hibiscus tiliaceus	X	X		X	X	X	X	X	X	X	X	X			X	X	X	X	X	X	
Inocarpus fagifera									X											X	
Jatropha curcas			X															X		X	
Leucaena insularum					X		X	X	X			X			X	X	X	X	X	X	
Leucaena leucocephala	X	X	X	X	X	X	X	X	X	X	X		X		X	X	X			X	

Table 1B. Distribution of tree species on the Tongatapu outliers

	Toketoke	Tufaka	Polo'a	Alakipeau	Fafa	Makaha'a	Pangaimotu	Manima	Oneata	Malinoa	Monuafe	Velitoa Hihifo	Velitoa Hahake	Mokotu'u	Onevai	Onevao	Motutapu	Fukave	Nuku	Ata	Tau
Lumnitzera littorea								X													
Mangifera indica			X				X						X				X			X	
Morinda citrifolia			X	X	X	X	X	X	X	X		X	X		X	X	X	X	X	X	
Musa x paradisiaca					X		X		X											X	
Neisosperma oppositifolia			X		X	X	X	X	X	X					X		X	X	X	X	
Pandanus tectorius	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X	X
Persea americana																				X	
Phaleria disperma					X	X	X		X			X	X			X	X	X	X	X	X
Pipturus argentus v.lanosus							X														
Pisonia grandis	X			X		X				X			X	X	X	X	X	X	X	X	X
Pittosporum arborescens							X	X	X	X					X		X			X	
Planchonella costata													X				X	X	X	X	
Plumeria acuminata							X					X									
Plumeria rubra																X	X			X	
Pometia pinnata			X						X											X	
Premna serratifolia			X	X			X								X		X	X		X	
Psidium guajava			X	X	X	X	X	X	X			X	X			X	X			X	
Rhizophora mangle			X			X	X								X						
Rhizophora stylosa			X				X								X						
Rhus taitensis							X	X	X							X	X				
Santalum yasi							X		X												
Spondias dulcis																			X		
Syzygium clusiifolium					X		X	X	X									X			
Syzygium richii							X										X		X		
Tamarindus indica																				X	
Tarenna sambucina							X		X												
Terminalia littoralis			X		X		X								X	X	X	X	X	X	X
Thespesia populnea			X	X	X	X	X	X	X		X	X	X		X	X	X	X	X	X	
Tournefortia argentea		X	X	X	X		X	X	X	X		X			X	X	X		X	X	X
Vavaea amicorum																	X			X	
Vitex trifolia		X	X	X	X	X	X	X	X		X	X			X	X					
Ximenia americana										X	X				X	X	X			X	
Xylocarpus moluccensis			X				X											X	X		
Xylosma simulans			X	X																	
unidentified						1							1		1						

Table 2. Distribution of shrub species on the Tongatapu outliers

	Toketoke	Tufaka	Polo'a	Alakipeau	Fafa	Makaha'a	Pangaimotu	Manima	Oneata	Malinoa	Monuafe	Velitoa Hihifo	Velitoa Hahake	Mokotu'u	Onevai	Onevao	Motutapu	Fukave	Nuku	Ata	Tau
Acronychia niueana					X																
Aglaia saltatorum							X						X								
Alyxia stellata																				X	
Ananas comosus			X																		
Bambusa vulgaris							X											X			
Bougainvillea glabra							X											X			
Caesalpinia bonduc					X		X		X						X					X	
Cestrum diurnum						X															
Clerodendrum inerme		X	X	X	X	X	X	X	X	X	X	X			X		X	X	X	X	X
Codiaeum variegatum							X														
Colubrina asiatica	X	X	X	X	X	X	X	X	X	X	X	X			X	X	X	X	X	X	X
Cordyline fruticosa	X		X	X			X		X	X										X	
Crinum asiaticum			X		X	X	X		X			X			X	X		X	X	X	
Derris trifolia			X		X		X	X	X												
Desmodium umbellatum	X																				
Furcraea foetida		X	X				X								X						
Gardenia taitensis								X									X				
Hibiscus manihot									X												
Hibiscus rosa-sinensis					X		X		X			X									
Indigofera suffruticosa			X		X	X	X	X	X			X	X			X		X		X	
Ipomoea batatas																				X	
Jasminum didymum	X	X	X	X	X	X	X	X	X						X	X	X	X	X		
Jasminum simplicifolium															X		X		X		
Lantana camara		X	X	X	X	X	X	X	X		X	X	X			X	X	X	X	X	
Macropiper puberulum						X	X										X	X		X	
Malvaviscus arboreus																		X		X	
Manihot esculenta			X				X		X				X			X			X	X	
Melia azedarach		X																			
Micromelum minutum																	X	X	X	X	
Pemphis acidula	X		X	X											X			X	X	X	
Ricinus communis													X								
Rosa sp.					X																
Saccharum sp.																				X	
Scaevola sericea	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X	X
Sophora tomentosa					X		X											X			
Suriana maritima		X			X					X					X		X	X	X	X	X
Triumfetta rhomboidea			X																		
Wollastonia biflora	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X	
Waltheria americana				X																	
unidentified					1	1	1				1				1	1					

Table 3A. Distribution of herb species on the Tongatapu outliers

	Toketoke	Tufaka	Polo'a	Alakipeau	Fafa	Makaha'a	Pangaimotu	Manima	Oneata	Malinoa	Monuafe	Velitoa Hihifo	Velitoa Hahake	Mokotu'u	Onevai	Onevao	Motutapu	Fukave	Nuku	Ata	Tau
Achyranthes aspera																				X	
Ageratum conyzoides						X															
Alocasia macrorrhiza																				X	
Amaranthus viridus					X																
Amylotheca isularum								X	X												
Apium leptophyllum			X		X		X		X									X		X	
Asclepias curassavica						X	X														
Asparagus sp.									X						X	X					
Bidens pilosa	X		X	X	X	X	X	X									X		X	X	
Capsicum frutescens			X															X			
Cassia occidentalis			X													X					
Cassia oppositifolia																				X	
Cassia tora			X														X				
Catharanthus roseus					X		X		X		X	X	X		X	X		X	X		
Centella asiatica				X			X	X													
Coleus amboinicus							X														
Colocasia esculenta							X		X											X	
Commelina diffusa			X																	X	
Crassocephalum crepidioides					X		X														
Desmodium incanum					X		X	X	X			X	X			X	X			X	
Desmodium heterocarpon			X																		
Elephantopus mollis																X					
Emilia sonchifolia			X		X	X	X	X	X			X	X			X	X		X	X	
Erigeron sumatrensis			X		X	X		X								X					
Euphorbia atoto		X	X	X	X	X	X	X	X	X	X	X	X		X	X		X	X	X	X
Euphorbia cyathophora						X			X												
Euphorbia hirta			X		X	X	X	X	X			X	X			X	X	X	X	X	
Euphorbia prostrata							X									X	X	X	X	X	
Helianthus sp.							X														
Hedyotis foetida	X			X																	
Lepidium virginicum			X				X										X	X	X	X	
Ludwigia octovalvis													X								
Malvastrum coromandelianum			X						X			X	X		X	X	X	X		X	
Mimosa pudica			X																		
Oxalis corniculata				X			X														
Phaseolus lathyroides			X																		
Phyllanthus prob. annuus							X						X					X		X	
Plantago lanceolata					X		X	X	X												

Table 3B. Distribution of herb species on the Tongatapu outliers

	Toketoke	Tufaka	Polo'a	Alakipeau	Fafa	Makaha'a	Pangaimotu	Manima	Oneata	Malinoa	Monuafe	Velitoa Hihifo	Velitoa Hahake	Mokotu'u	Onevai	Onevao	Motutapu	Fukave	Nuku	Ata	Tau
Portulaca oleracea			X									X	X	X	X				X	X	X
Rivina humilis		X	X	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X		
Sesuvium portulacastrum	X		X	X				X			X	X	X		X	X				X	
Sida rhombifolia			X				X					X	X			X		X			
Solanum nigrum															X			X		X	
Sonchus oleraceus				X			X					X									
Spermacoce assurgens					X	X	X	X	X							X	X		X	X	
Stachytarpheta urticaefolia			X	X	X	X	X	X	X			X	X			X	X				
Synedrella nodiflora			X				X	X					X					X		X	
Tacca leontopetaloides																				X	
Taxacum officinale			X				X					X	X			X	X			X	
Triumfetta procumbens	X				X															X	X
Youngia lyrata			X													X				X	
unidentified						1															

Table 4. Distribution of vine species on the Tongatapu outliers

	Toketoke	Tufaka	Polo'a	Alakipeau	Fafa	Makaha'a	Pangaimotu	Manima	Oneata	Malinoa	Monuafe	Velitoa Hihifo	Velitoa Hahake	Mokotu'u	Onevai	Onevao	Motutapu	Fukave	Nuku	Ata	Tau
Abrus precatorius			X	X	X						X				X					X	
Canavalia cathartica			X				X													X	
Canavalia rosea		X	X	X	X	X	X	X		X	X	X	X		X	X		X			
Canavalia sericea	X	X	X	X	X	X	X	X		X	X	X	X		X	X		X		X	X
Cassytha filiformis		X			X	X	X	X	X		X	X			X		X	X		X	X
Cucurbita pepo													X		X						
Dioscorea alata							X													X	
Dioscorea bulbifera			X															X			
Hoya australis	X		X	X			X														
Ipomoea littoralis							X								X		X				X
Ipomoea macrantha					X		X		X									X		X	X
Ipomoea pes-caprae		X			X		X	X	X	X	X	X			X	X	X	X	X		X
Merremia peltata																			X		
Mucuna gigantea					X	X	X											X			
Passiflora edulis					X	X	X		X											X	
Passiflora foetida			X	X	X	X	X	X	X		X	X	X			X		X		X	
Passiflora quadrangularis	X		X																		
Passiflora triloba			X														X	X			
Phaseolus aureus												X			X						
Pueraria lobata																	X			X	
Vanilla planifolia			X																		
Vigna marina					X	X		X	X				X		X	X		X	X	X	X
unidentified						1															

Table 5. Distribution of grass and sedge species on the Tongatapu outliers

	Toketoke	Tufaka	Polo'a	Alakipeau	Fafa	Makaha'a	Pangaimotu	Manima	Oneata	Malinoa	Monuafe	Velitoa Hihifo	Velitoa Hahake	Mokotu'u	Onevai	Onevao	Motutapu	Fukave	Nuku	Ata	Tau
Brachiara mutica															X						
Cenchrus echinatus			X		X		X					X	X					X	X	X	
Cyperus rotundus			X						X									X			
Digitaria horizontalis			X																	X	
Digitaria setigera							X												X	X	
Eleusine indica			X				X						X						X	X	
Eragrostis amabilis																X					
Fimbristylis cymosa					X			X		X								X			
Ischaemum mirinum		X		X			X	X		X		X	X		X	X	X				
Kyllinga brevifolia			X										X							X	
Lepturus repens			X			X		X	X		X	X								X	
Mariscus javanicus		X		X		X						X	X			X				X	
Panicum maximum	X	X	X	X	X	X	X	X	X	X	X	X	X			X				X	
Paspalum conjugatum			X				X											X	X		
Sporobolus virginicus		X		X	X	X	X			X		X			X	X	X	X	X	X	X
Thuarea involuta		X		X	X	X	X	X	X	X	X				X	X		X	X	X	X
unidentified																	1				

Table 6. Distribution of fern species on the Tongatapu outliers

	Toketoke	Tufaka	Polo'a	Alakipeau	Fafa	Makaha'a	Pangaimotu	Manima	Oneata	Malinoa	Monuafe	Velitoa Hihifo	Velitoa Hahake	Mokotu'u	Onevai	Onevao	Motutapu	Fukave	Nuku	Ata	Tau
Asplenium nidus					X		X		X												
Polypodium scolopendria	X		X	X	X	X	X	X	X	X		X	X		X			X		X	

Table 7. Numbers of species of vascular plants on the Tongatapu outliers

ISLAND	Area (ha.)	No. species	Trees	Shrubs	Herbs	Vines	Grasses /sedges	Ferns
Toketoke	0.26	24	8	7	4	3	1	1
Tufaka	0.67	26	6	9	2	4	5	0
Polo'a	1.11	89	32	15	23	10	8	1
Alakipeau	0.37	46	17	9	9	5	5	1
Fafa	8.56	72	26	14	14	10	5	2
Makaha'a	2.54	63	25	11	12	8	5	1
Pangaimotu	17.14	115	47	21	25	12	8	2
Manima	2.1	59	24	9	13	6	6	1
Oneata	5.55	77	35	14	15	6	5	2
Malinoa	0.88	33	17	6	1	3	5	1
Monuafe	0.3	30	11	6	4	6	3	0
Velitoa Hihifo	0.41	48	14	8	13	6	4	1
Velitoa Hahake	0.24	50	16	9	15	5	6	1
Mokotu'u	0.008	4	2	0	2	0	0	0
Onevai	14.34	63	31	10	8	9	4	1
Onevao	2.3	45	26	9	18	5	6	1
Motutapu	7.81	67	36	11	12	5	3	0
Fukave	12.52	73	27	16	13	10	6	1
Nuku	4.61	51	20	12	10	3	6	0
Ata	15.41	103	40	18	24	9	10	1
Tau	0.85	24	9	4	3	6	2	0

Plate 1: *Pandanus* outposts, east shore of Ata.

Plate 2: *Rivina* under *Cocos* woodland, Fukave.

Plate 3: *Canavalia* and *Thuarea* colonising loose sand, west shore of Ata.

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KIRIBATI AGROFORESTRY:

TREES, PEOPLE AND THE ATOLL ENVIRONMENT

BY R. R. THAMAN

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KIRIBATI AGROFORESTRY:

TREES, PEOPLE AND THE ATOLL ENVIRONMENT

BY R. R. THAMAN

INTRODUCTION

Agroforestry, the planting and protection of trees and tree-like plants as integral components of a polycultural agricultural system, has always been central to the economic, cultural and ecological stability of the Kiribati society. This paper focuses on Kiribati agroforestry, and on the role trees play as: 1) integral components of polycultural agricultural systems; 2) symbols of stability and cultural wellbeing; 3) sources of a diverse range of subsistence and commercial products, the imported substitutes for which would be either too expensive or unavailable to most people; and 4) ecologically important components of agricultural systems which, if lost, would lead to irreversible environmental degradation and resultant cultural deterioration. Two islands of Kiribati, Tarawa and Abemama serve as case studies of Kiribati village-level agroforestry. The findings are based on a ten-day reconnaissance survey of agroforestry on Tarawa and Abemama in 1984, a subsequent visit in early 1989, and a survey of the available literature.

TREES AS SYMBOLS OF ECOLOGICAL AND CULTURAL STABILITY

Although symbols of ecological and cultural stability, forests and trees are rapidly disappearing from the earthscape. As argued by Thaman and Clarke (1987), the replacement of long-lived trees in diversified mixed stands by shorter-lived trees and other types of plants in monocultural stands or by totally artificial landscapes, although yielding undeniable short-term benefits to mankind, severely deteriorates human habitats on the earth.

DEFORESTATION IN THE PACIFIC ISLANDS

Although economically and ecologically precious tropical forests remain on some of the larger Pacific islands, and small areas of mangrove and ubiquitous strand forest have been preserved on others, deforestation in the Pacific is proceeding at a frightening rate. Forests, both primary and secondary, continue to be transformed into degraded savannas and fern-grasslands, mangroves into housing and industrial estates or other lifeless land-sea interfaces, polycultural tree-studded traditional agroforested gardens into monocultural plantations, and urban areas divested of their remaining trees to make way for industrial, commercial, and residential areas or to fuel the cooking fires or erect the squatter housing of low-income families. The trends are the same from the high continental islands of Melanesia to the smallest atoll islets of Polynesia and Micronesia (Thaman and Clarke, 1987).

Deforestation has led to severe erosion in Wallis and Futuna, the Cook Islands, French Polynesia and Hawaii where most of the indigenous forest has been removed, leaving degraded fernlands and grasslands no longer suitable for agriculture (Kirch, 1982:4). Flenley and King (1984) go as far as suggesting that deforestation was responsible for the collapse of the pre-European megalithic culture on Easter Island,

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a view supported by McCoy (1976 in Kirch, 1982:4), who argues that the "radical reduction of forest, shrub, and grassland communities, following over-exploitation and misuse by man", was responsible for a change from open-field cultivation to protected stone garden enclosures (manavai). Similarly, drastic deforestation of the central plateau on the Hawaiian island of Kaho'olawe, due to shifting cultivation and increasing population pressure between AD 1375 and 1600, reportedly led to a "dramatic population crash" and the total abandonment of the interior of the island by 1700 (Hammon, 1980; Kirch, 1982:4). Although, today, some countries and territories have conservation legislation and forestry ordinances, trees are cleared and forest products continue to be shipped off for a fraction of the world market price, while Japan, South Korea, China, and other countries continue to protect their forest resources and to implement major reforestation efforts (Richardson, 1981).

The situation is perhaps more critical in Kiribati, where land area is severly limited and useful trees have been removed in historical times to make way for the expansion of coconut plantations for the production of copra for export. The widespread removal of coastal strand species and mangroves for fuelwood and other cultural purposes continues in many areas, and "agrodeforestation" (Thaman, 1989ab), the removal, neglect, or the failure to replant trees as integral parts of the Kiribati agricultural system, continues unabated, almost completely unheeded by policy makers in the agricultural and forestry sectors. As Chambers (1983) argues, trees and tree planting as traditional components of agricultural systems have been ignored in institutionalised rural development because they "fall into the gaps" between the traditional sectoral responsibilities of "agriculture" and "forestry".

AGRODEFORESTATION AS AN ISSUE

Although deforestation, as such, has received most attention globally, probably of tantamount importance is "agrodeforestation" in the forms of both declining tree planting and the elimination of trees from agricultural and urban landscapes. Trees that have, for generations, provided food, timber, firewood, medicines and served other important cultural and ecological functions, as integral components of polycultural agricultural systems, are increasingly not being replaced or protected by the present generation. Although some countries have increasingly effective systems of forestry reserves, conservation areas, or national parks, few, if any, have legislation or programmes prohibiting the cutting, or promoting the replanting of important or endangered tree species as part of agricultural or other modern-sector development. Thus, agrodeforestation continues, with little or no official recognition or resistance to it.

The situation is not yet beyond hope as it appears to be in some areas of the world because most traditional agroforestry strategies of the Pacific Islands have been preserved, if only in relict form. Nonetheless, increasing agrodeforestation and the gradual disappearance of time-tested agroforestry systems in the face of monocultural expansion of agriculture and commercial livestock production, rapid population growth, demands for fuel, continued urbanization, and the "commercial imperative" (Tudge, 1977) are the dominant trends that will only be reversed by deliberate planning and action (Thaman and Clarke, 1987).

NATURE OF TRADITIONAL AGROFORESTRY IN THE PACIFIC ISLANDS

In traditional Pacific Island "development", forestry, agriculture, housing, medicine, and the production of a wide range of material goods were not compartmentalized into "sectors"; rather they were generally part of integrated

agroforestry systems or strategies tailored to the environmental and societal needs of each island ecosystem. Trees, of course, were major components of such sustainable agroforestry systems (Thaman and Clarke, 1987).

In terms of composition and spatial organisation, all traditional agroforestry systems, from the highlands of Papua New Guinea to the smallest atoll countries, exhibited a high degree of interspecies diversity, incorporating a wide range of cultivated and protected indigenous and exotic species, ranging from some 75 species commonly encountered on atolls, such as in Kiribati which have among the poorest floras on earth, to over 300 widespread species species in the larger-island agroforestry systems of Fiji, Vanuatu, Solomon Islands, and Papua New Guinea. Species include not only traditional staple tree crops such as coconuts, breadfruit, and bananas or plantains intercropped with ground staples and supplementary ground crops, but also a wide range of fruit and nut trees and other useful trees and plants which are either deliberately planted, encouraged and protected in the regeneration of fallow regrowth, or spared when clearing new garden plots.

Moreover, for most traditional tree cultigens and non-tree understory cultigens, for many recently-introduced cultigens, and for a lesser number of indigenous species found in Pacific island agroforestry systems, there is also a high degree of intraspecies diversity, with a wide range of named, locally differentiable cultivars or varieties. Within a given species, these cultivars have variable yield characteristics and seasonality, thus spreading yield distribution and seasonal surpluses more evenly. Similarly, as has been found true in other parts of the world, different cultivars have differential resistence to pests and diseases and to tropical cyclone damage, saltwater incursion and salt spray and drought; differential ecological tolerance ranges in terms of adaptability to different soil types, shade and hydrological regimes; and differential utility (for example, in Kiribati some coconut cultivars are used purely as drinking nuts, some for the flesh, and some for the large shells or the coir which can be used for vessels or for rope respectively).

Also seen as integral components of the broader village agroforestry systems are: 1) secondary or fallow forest areas, indigenous stands of tropical rainforest, and mangrove or coastal strand forest which border or fall within the matrix of active garden or fallow areas; 2) permanent, often sacred, tree groves of primarily planted useful trees in garden areas or surrounding villages; and 3) trees planted in home gardens in nucleated villages or around isolated dwellings. Together these diverse arboreal resources present an image of agroforestry far different and far more polycultural and utilitarian than the predominant view of "modern" agroforesters which commonly sees "agroforestry" as constituting the intercropping of export cash crops such as cocoa, coconuts, coffee or bananas with selected ground or shade crops; cattle under coconuts; the promotion of fuelwood plantations or wood lots; or the intercropping of exotic forest species with export or subsistence ground crops, with virtually no mention of the hundreds of other useful plants and wild animals that are integral to the traditional systems that they often irreversibly replace.

In terms of the more specific utilitarian attributes of individual Pacific agroforestry systems, Table 1 is an attempt to show the multi-functional nature of these systems as well as the value of the individual arboreal components. Although modern agroforesters and horticulturalists may see native forests; silvicultural tree plantings; coconut, oil palm, cocoa, coffee, or banana plantations; or orange, avocado or macadamia orchards in terms of their economic value, or, possibly, even in terms of their ecological, recreational, or nutritional values, it is clear the Pacific island agroforesters perceived arboreal resources to be far more multi-purposeful.

In terms of the ecological value of trees, shade, for example, is critically important

to humans, plants, and animals, especially in open savanna lands, in highly reflective low-lying coral island and lagoonal environments, and in villages and urban areas; damage from wind, erosion, and flood are increased when forests are removed; and mangrove and coastal strand forests stabilize tidal-zone soils and reduce the impact of storm surge and ocean salt spray.

Soil improvement is another area where trees are of critical importance, especially given the high cost of fossil-fuel-dependcnt inorganic fertilizers and recent concern as to the detrimental impact on soil of long-term use of such fertilizers. In the case of Kiribati, with among the poorest soils on earth, in terms of both available soil nutrients and organic material, this function takes on much greater importance. The value of forests and trees as habitats for plants and animals, many of which are of considerable subsistence and commercial value, cannot be overstated (Thaman and Clarke, 1987).

There is no need to examine the importance of timber, except to emphasize that trees are of critical importance in the informal sector in most countries for house construction, fencing, boatbuilding, toolmaking, weaponry, making containers, fishing gear, cooking equipment, and handicrafts (Table 1).

Foods from trees are of immense value, whether as staples, supplementary sources, or occasional snacks and famine foods. The nutritional importance of dominant staple tree crops, such as coconut, breadfruit, bananas and plantains, sago palm, and Pandanus spp. and the wide range of fruit and nut trees found throughout the Pacific have been widely stressed elsewhere and need no further mention (Parkinson, 1982; Coyne, 1984; Thaman, 1979, 1982ab, 1983, 1985, Yen, 1980ab). Supplementary foods and snacks are described by Thaman (1976, 1976/77, 1982ab) for Tonga and Fiji and other Pacific Islands and by Clarke (1965, 1977) for a highland Papua New Guinean community. Powell (1976) provides a comprehensive coverage of wild-food use and other important aspects of ethnobotany for the entire island of New Guinea.

Table 1. Ecological and cultural functions and uses of trees in agroforestry systems in the Pacific islands, based on fieldwork in Papua New Guinea, Solomon Islands, Vanuatu, Fiji, Tonga, Western Samoa, Kiribati, and Nauru.

ECOLOGICAL		
Shade	Soil Improvement	Animal/Plant Habitats
Erosion Control	Frost Protection	Flood/Runoff Control
Wind Protection	Wild Animal Food	Weed/Disease Control
CULTURAL/ECONOMIC		
Timber(commercial)	Broom	Prop or Nurse Plants
Timber(subsistence)	Parcelisation/Wrapping	Staple foods
Fuelwood	Abrasive	Supplementary Foods
Boatbuilding(canoes)	Illumination/Torches	Wild/Snack/Emergency Foods
Sails	Insulation	
Tools	Decoration	Spices/Sauces
Weapons/Hunting	Body Ornamention	Teas/Coffee
Containers	Cordage/Lashing	Non-alcoholicBeverages
Woodcarving	Glues/Adhesives	Alcoholic Beverages
Handicrafts	Caulking	Stimulants
Fishing Equipment	Fibre/Fabric	Narcotics
Floats	Dyes	Masticants

Toys	Plaited Ware	Meat Tenderizer
Switch for Children/Discipline	Hats	Preservatives
Brush/Paint Brush	Mats	Medicines
Musical Instruments	Baskets	Aphrodisiacs
Cages/Roosts	Commercial/Export Products	Fertility Control
Tannin	Ritual Exchange	Abortificants
Rubber	Poisons	Scents/Perfumes
Oils	Insect Repellents	Recreation
Toothbrush	Deodorants	Magico-religious
Toilet Paper	Embalming Corpses	Totems
Fire Making	Dancing Grounds	Subjects of Mythology
		Secret Meeting Sites

Source: Adapted from Thaman and Clarke, 1987.

It is important to stress, however, that although many tree foods are energy-rich in carbohydrates and/or vegetable fats, it is in other nutritional essentials such as vitamins and minerals and fibre that they often excel in comparison with the ubiquitous root-crop staples and other annual non-arboreal plants. For example mango, papaya, and some Pandanus spp. are excellent sources of provitamin A; Canarium spp., Inocarpus fagifer, and avocado (Persea americana) of B-complex vitamins; guava, mango, papaya, and Citrus spp. and other lesser known species, such as beach mulberry (Morinda citrifolia) and bush hibiscus spinach (Hibiscus manihot), of vitamin C and/or iron; and most seeds or green leaves (for instance, from Ficus spp., Gnetum gnemon, which also provides edible seeds, and Moringa oleifera) are good sources of plant protein and a range of other micronutrients necessary for optimum health (Thaman and Clarke, 1987; Thaman, 1983). Spices and sauces from tree products can also be of great nutritional importance.

Wild food and other valuable products are also lost to subsistence communities when the diversity of plants and animals that supplied them disappear along with the forest that served as their habitats (Clarke, 1965; 1977; Thaman 1982a). Deforestation has severely restricted the habitats for wallabies and the valued cassowary bird of Papua New Guinea, and a great number of vertebrate and non-vertebrate wild animal foods and an even greater range of wild plant foods that contribute significantly to the dietary well-being of many Pacific islanders, particularly in the interior of large continental islands. The destruction of mangrove forests is of particular concern for coastal and atoll communities because of their importance in marine and estuarine food chains as well as being favoured habitats or nurseries for a wide range of fin-fish, molluscs, and crustaceans (Thaman, 1982a). The removal of trees such as Pisonia grandis, the favored nesting or rookery species of the black noddy tern (Anous tenuirostris), a delicacy reserved for important feasts in Kiribati and Nauru, also impoverishes traditional food systems.

Trees are also important sources of food and fodder for domesticated animals. Pisonia grandis leaves for example, are used as pig feed; Leucaena leucocephala leaves and pods are used widely for goats, pigs, and cattle; and coconuts and papaya are abundant and important animal foods throughout the Pacific.

In terms of other uses, the arboreal pharmacopoeia is widely known and valued by modern science and industry as well as by local inhabitants, with all parts of the Pacific possessing medicine-producing trees and associated plants. Wrapping materials includes coconut leaves, leaves of Artocarpus altilis, Musa cultivars, Hibiscus tiliaceus and Macaranga spp. Other leaves, notably Ficus spp., serve as effective abrasives. Dyes are derived from many sources, e.g., Bischofia javanica (a major red-brown dye for

tapa), Bruguiera spp. and Aleurites moluccana (black), Morinda citrifolia (yellow), and Bixa orellana (red)(Thaman and Clarke, 1987).

Perfumes or scents such as sandalwood are well known outside of the Pacific, while less cosmopolitan fragrances are derived from Cananga odorata and other scenting agents that are put into coconut oil from trees such as Pimenta, Plumeria, Pandanus and Gardenia spp., Parinari glaberrima, Aglaia saltatorum, Fagraea berteriana, and Calophyllum inophyllum (Thaman and Clarke, 1987). In Tonga, for example, there are over 50 species of sacred or fragrant plants, known as ʻakau kakala, which are central to the spiritual and economic fabric of Tongan society and which are planted or protected as integral components of Tongan agroforestry (Thaman, 1986, 1987a). Plants have similar spiritual value in Kiribati, with many featuring in Kiribati legends and cosmogeny and being used for scenting coconut oil and ceremonial body ornamentation (See Table 2).

These few examples from Table 1, show the utilitarian diversity and the economic and cultural value derived from trees and agroforestry in the Pacific, values that are rarely acknowledged in planning or project documents, but that would be extremely difficult or impossible to replace with imported substitutes. The elimination of such utilitarian and cultural diversity can only serve to lock Pacific societies more tightly into the vicious circle of economic and cultural dependency.

KIRIBATI AGROFORESTRY

The non-urban Pacific island agroforestry systems that operate under the most severe environmental constraints and population pressure are found on atolls. Atolls may, in fact, be the most intensively agroforested island type in the Pacific in terms of the relative importance of trees to non-trees within the system.

An excellent example of atoll-agroforestry is that practiced in Kiribati, where a wide range of cultivated and protected wild trees and a more limited number of non-tree plants and livestock are raised within a relatively dense and homogeneous matrix of coconut palms. Population pressure is high especially on the main island of Tarawa, where 17,921 people inhabit an area of only 920 ha, with the population density of the most populated islet, Betio, expected to reach densities rivaling Singapore by the year 1990 (Carter, 1984:231). Population densities on Abemama and other outer islands are significantly lower. The only agricultural export from Kiribati is copra, of which 5,682 tonnes valued at $A3,074,536 were exported in 1979 (Pargeter et al., 1984).

Environmentally, the atolls and table-reef islands of Kiribati are rarely more than 3 metres in elevation above high-tide level, with the true atolls surrounding large central lagoons. Their highly alkaline calcareous and rocky soils are among the most infertile on earth, with very low water-holding capacity, little organic material, few available soil macro- and micro-nutrients, apart from calcium, sodium, and magnesium, and restricted availability of iron and other micro-nutrients because of the high pH. Rainfall is extremely variable, with extended periods of drought being common. Ground water is brackish to slightly salty and subject to saltwater incursion. The islands, where one is never more than 0.5 kilometres from the sea, are susceptible to inundation by storm surge and tsunamis (seismic sea waves) and the constant effect of humid salt-spray-laden winds. As stressed by Small (1972:5): "all this adds up to a very difficult environment for plants, and produces problems for animals and man."

In terms of floristic diversity, as a result of small island size, distance from the Asian continent, relatively young geologic age of the islands, and harsh environmental conditions, there are estimated to be only 66 indigenous plant species, found in

Kiribati, none of which are endemic, and just under 300 total species, including exotics, mostly ornamentals and weeds, which have ever been reported to grow there (Fosberg and Sachet, 1987; Fosberg et al., 1979, 1982; Thaman, 1987b).

It is under these harsh conditions and a paucity of flora to choose from, that the I-Kiribati (people of Kiribati) have evolved their distinctive agroforestry system, which incorporates into a matrix of the superdominant coconut palm (Cocos nucifera): 1) indigenous species (almost exclusively ubiquitous pan-Pacific or pan-tropical, ocean-dispersed species); 2) selected aboriginally-introduced food plants, such as the staple giant swamp taro or babai (Cyrtosperma chamissonis) and pandanus or te kaina (Pandanus tectorius); 3) some recently-introduced exotics; and 4) settlements or villages and other urban features (Table 2).

Scattered throughout the matrix of the superdominant coconut or te ni (Cocos nucifera) are pandanus or te kaina (Pandanus tectorius), breadfruit or te mai (Artocarpus altilis), and the native fig or te bero (Ficus tinctoria), along with a wide number of pantropical strand species, such as Scaevola sericea, Tournefortia argentea, Guettarda speciosa, and Pemphis acidula.

Coconut Palms

Almost all coconut palms seem to have been planted either deliberately or accidentally by the I-Kiribati. The resultant agroforested landscape takes the form of a real forest, rather than an orderly plantation, because a great proportion of the trees are spontaneous occurrences of different heights and age-classes, rather than deliberately planted, equally-spaced trees of a single age class. On both the seaward and lagoon-side, coconuts lean outward interspersed with pan-tropical strand species, whereas in the higher central portions of the islands they generally form thick stands, with young coconut seedlings and other plants in various stages of growth often forming an almost impenetrable jungle that extends almost from the beach ramparts on the ocean side towards the centre of the islands. In many areas, plants suffer from excessive density, although towards the lagoon side, where most of the settlements and giant taro (babai) pits are found, the "forest" begins to thin out (Catala, 1957:22; Watters and Banibati, 1977:33). Moul (1957:1), however, found concentrations to be denser along lagoon shores and interspersed with young palms and pandanus on Onotoa atoll in southern Kiribati.

Sixteen locally recognized coconut cultivars are divided into two main categories according to whether the mesosperm is edible (te bunia) or non-edible (te ni), the latter term also applying to coconuts in general. Some are favoured for their juicy flesh, the quality and sweetness of their toddy and some for the quality of their fronds, coir from the husk, or wood for use as handicrafts and building materials (Catala, 1957:25-27).

Catala (1957:30-34) stressed the "extraordinary resistance of the palm" in Kiribati to prolonged drought and its ability to continue to produce inflorescences, which although incapable of producing commercial value copra, still produced the nutritionally essential toddy. The ability to withstand prolonged drought depends on the nature of soils, the degree of salinity of groundwater, the nature of tides during droughts, and the sporadic occurrence of fire during drought periods. Despite this incredible resistance to drought and increasing salinity, the production of most palms, most notably copra production, is severely affected by drought, although palms around village sites, beside babai pits or in abandoned babai pits, and around inland ponds seem to be affected only minimally by drought because of proximity to the freshwater lens or the presence of greater domestic and organic waste near villages and babai pits. Watters and Banibati (1977:33) reported that, after a prolonged drought in the early

1970s, only 44.2% of mature coconut palms surveyed on Abemama were bearing in 1972.

In the terms of tree density, a transect across Bikenibeu islet, Tarawa contained 138 irregularly spaced palms in an area of 5,950 m^2, a very high density of 231 per ha (a fully stocked regularly spaced copra plantation in Tonga would have a density of only 157 per ha). In this same area, 11 pandanus trees, most of them concentrated in the mid-island portion or toward the lagoon and village end of the transect, were also inventoried. Nearer to village sites, the density was considerably lower, with fourteen surveys giving an average density of only 155 palms per ha, not counting other important trees. For example, one village, covering an area of some 10,750 m^2 had only 100 coconuts, a density of 93 per ha, as well as 36 breadfruit trees. For village areas, the average density ranged from 80 to 150, whereas densities were from 200 to 350 in bush garden areas.

The overall estimated density of coconut coverage for the estimated 2,000 ha area of Tarawa Atoll (1,600 ha, after deducting 20% for uncultivated areas under mangrove, swamp, roads, etc.), was 231 in the mid-1950s, thus giving an estimated 369,600 palms for the productive area. Subtracting two trees for every five people (955 trees) for toddy production left a total of 368,645 nut-producing trees, which produced an estimated 23.1 nuts per year, or 8,517,000 nuts available for consumption by humans, animals, for copra production, and for other uses such as making perfume and oil. The estimated annual per capita consumption at the time was four nuts per day for humans and three for pigs (Catala, 1957:40-45).

A more recent study by Watters and Banibati (1977:35) suggests that density of coconut palms on rural Abemama was even higher at 321 palms per ha, with densities of bearing palms being 151.8 (given a figure of 47.3% bearing palms). The estimates of nuts per bearing tree of 17.8 was somewhat lower than Catala's, possibly because the survey was conducted after an extended drought.

For toddy (karewe) production, which perhaps nowhere has such fundamental importance as in the harsh environment of Kiribati, the flower spathes of selected trees are cut and bound and tapped twice a day, once in the morning and once in the afternoon, yielding approximately two coconut shells of liquid per day. A dietary staple for most I-Kiribati households, especially in times of severe drought when palms produce few fruit, fresh toddy is drunk daily by most I-Kiribati. Toddy is also fermented to make a vitamin B-rich (one-third the level found in brewer's yeast) drink (te maning) of varying alcoholic content, a boiled-down syrup (kamaimai), which can be kept without fermenting, and a solid caramelised form (kareberebe)(Catala, 1957:44-46).

In rural areas, in particular, coconut flesh is the major source of dietary fat and a major source of calories, as well a contributing some iron, fibre, and other nutrients, and is prepared and consumed in countless ways. Toddy is particularly rich in energy and vitamin C and has significant amounts of vitamin B and iron (Pargeter et al., 1984:10-15). Bayliss-Smith's (1982:62) study of Ontong Java atoll in Solomon Islands, stresses the dietary importance of coconut, which contributed 21% of all calories directly, as well as the copra, which provided the cash to purchase another 25% of the total calories consumed. In addition to its critical dietary importance, the coconut palm is used in a myriad of other ways to produce products of economic and cultural importance, the imported substitutes for which would either be too costly or unobtainable for most I-Kiribati (Table 2).

Pandanus

After the coconut, the pandanus or te kaina (Pandanus tectorius) is the most

important tree of Kiribati agroforestry systems, with almost two hundred different recognized cultivars, many of which may be exclusive to a given village or family (Overy et al., 1982; Luomala, 1953). Catala (1957:51) reports, however, that only 16 names were widely recognised on Tarawa.

Because pandanus will grow in very poor or thin soils, it can be found growing almost anywhere on atoll islets. In ecological surveys of pandanus, Catala (1957:52) found that for Tarawa atoll there was an equal density of pandanus, whether it was on the ocean or lagoon side, or, in the interior, although it grew more successfully where coconut density was lower, particularly in marshy areas or along the lagoon edge where pandanus seems to have a definite advantage over the coconut. Moul (1957) also found pandanus present in most vegetation associations on Onotoa atoll.

Although natural stands commonly occur in swampy areas, in coastal littoral forests and bush plantations which have been neglected for extended periods, the majority of pandanus in garden lands or around villages or residences are planted and owned by individuals (Luomala, 1953:83). Because pandanus propogated from seeds will rarely reproduce desired characteristics, almost all planted pandanus are started from cuttings, ideally cuttings which already bear the beginnings of adventitious roots. At times, new trees will be mulched with leaves of Guettarda speciosa or other plants, and coverered with black topsoil, as well as receiving compost or attention. Frequent tamping around young plants, even after they are fully established, is carried out to obtain low, easy-to-harvest high-yielding trees. Given optimum light availability and care, trees near villages can bear as soon as tens months after planting, whereas they may take up to more than a year in bush gardens (Catala, 1957:53-54).

The fruit of pandanus is a very important part of the I-Kiribati diet; the tree also provides raw material for a wide range of plaited ware, construction materials medicines, decorations, parcelisation, perfumes, and other uses, as well as being the I-Kiribati ancestral tree, from which, according to mythology, the progenitors of the I-Kiribati came (Luomala, 1953:83).

The fleshy parts or drupes of the ripe fruits are consumed raw, as well as being prepared or included in other dishes in a variety of ways. Some of the commonest preparations are te tangauri, te tuae, and te karababa. Te tangauri, a paste made from a mixture of a puree of the fresh fruit and grated coconut, can be eaten fresh or dried in the sun. Te tuae, is prepared by cooking the fruit, removing most of the fibre, and making a paste, which is then spread on leaves and dried in the sun. The dried paste, which is then cut into pieces for further desiccation, will keep for years, constituting a food reserve which can be used on long voyages or prepared at a later time by softening in and/or prepared with coconut milk or grated coconut. Te karababa is prepared by cooking the drupes, mashing them and mixing them with grated coconut. The resultant product is then eaten after being spread in the sun for further desiccation, or is further processed into te kabubu by toasting and grinding into flour, which keeps for long periods and which may be eaten straight or prepared as an ingredient in a range of dishes, including te korokoro, in which te kabubu is mixed with kamaimai (toddy molasses)(Catala, 1957:56-58).

Pandanus leaves are used in the production of thatching, roofing, a range of fine and everyday mats, hats, sails (in the past), cigarette wrappings, food wrappers, caulking material, and baskets for babai compost. The trunk and adventitious roots are used in house and general construction, with particular cultivars being best for different uses (Luomala, 1953; Catala, 1957; Overy et al., 1982)(Table 2).

Breadfruit

The next most important cultivated plant is the breadfruit or te mai, of which there are two distinct species, the common breadfruit (Artocarpus altilis) and the Mariannas breadfruit (A. mariannensis), plus a hybrid of the two (Fosberg et al., 1979; Fosberg and Sachet, 1987; Thaman, 1987b). Although well-adapted to the atoll environment, its distribution seems to be directly related to the salinity of groundwater, being planted primarily in villages or their immediate vicinity, and occasionally along roadsides, particularly on the more protected lagoon side of the islands. Moul (1957:11) reported that it was very common along village streets on Onotoa, and the canopy of one of the most extensive breadfruit groves on Tarawa almost covers the main road through the chiefly village of Eita.

Although much less common, breadfruit rivals pandanus in subsistence importance in some areas. Whereas pandanus is an important component of the "bush" flora, often forming pure stands, breadfruit is rarely found in the heart of the bush (Catala, 1957:61), but forms a major, often dominant component of the vegetation around villages such as Eita and Betio on Tarawa. In one village on Tarawa, with a population of 115 (22 families), Catala (1957:64) counted 93 trees, all of which belonged to the person or household who planted them, even if the planter moved to another village. The number of trees per household varied from 0 to 11, with the mode being 4 (Catala, 1957:Table X).

Like pandanus, breadfruit are almost always deliberately planted in holes, or circular well-like structures, filled with waste, including the dead leaves of coconut and breadfruit and the leaves of te mao (Scaevola sericea), te ren (Tournefortia argentea), te uri (Guettarda speciosa), and te non (Morinda citrifolia), and often topped with black topsoil found under Guettarda speciosa (Catala, 1957:64; Moul, 1957; Small, 1972). Under favourable conditions, trees may reach over 20 metres in height, with trunks almost two metres in circumference, although under less favourable conditions, trees may only reach 8 to 10 metres and one metre in circumference (Catala, 1957:64).

Of the major economic plants, the breadfruit seems to have the least resistance to prolonged drought. Sabatier (1939 in Catala, 1957:61)), says that breadfruit trees survive with difficulty in the drier southern islands and "are practically exterminated every ten years." Moul (1957:11) reports that a significant proportion died during the prolonged drought of 1949-50. It generally bears for the nine months from May to January, during which time fruit is often very abundant, being eaten ripe, both raw and cooked, depending on the variety, as well as being cooked, crushed and preserved by drying as te kabuibui ni mai or te tuae n-te mai.

Young leaves and buds of breadfruit are used medicinally to cure ear infections and conjunctivitis respectively, the leaves for food parcelisation and fertiliser or compost for babai and other plants, and the wood for outrigger canoe hulls and fishing floats (Catala, 1957:65-66).

Other Cultivated Fruit Trees

Other commonly cultivated fruit trees are papaya, te mwemmweara or te babaia, banana and plantain cultivars or te banana, the native fig or te bero (Ficus tinctoria), the common fig or te biku (Ficus carica), and the lime or te raim (Citrus aurantiifolia). Occasionally lemon trees or te remen (Citrus limon) are found, and guava and mango have been introduced but are rare, and, in the case of mango, survive with difficulty (Table 2).

Papayas are particularly common in villages, and, where well cared for and mulched, are healthy and produce good fruit, which is eaten raw when ripe, especially

by children, and cooked green with coconut milk. In a village of 23 households, with a population of 115, Catala (1957:Table X) found 111 papayas, amounting to just under one tree per person, although the age and productivity of individual trees were not indicated.

Bananas and plantains, of which there seem to be two main and two less common cultivars (Table 2), are occasional to common, although much more common on wetter islands in north Kiribati, such as Makin and Butaritari, and in southern Tuvalu, where the main island of Funafuti (meaning the "place of the banana") is renown for its extensive banana plantings. Bananas are commonly grown around houses in villages and occasionally planted in abandoned babai pits or in specially dug banana pits, a common practice at mission settlements and boarding schools. Although most commonly grown in pits, bananas and plantains, are normally not planted in flooded soil, as is babai, but in slightly higher parts of pits or in pits which have been partially filled.

Where well looked after, bananas grow well and are a favoured staple when eaten green or as a fruit when ripe. If grown as a "pit plantation", it is usually necessary to dig a rather deep trench around the pit to keep coconut roots out. A layer of dark soil collected from under Guettarda and Scaevola is added along with composting and rusted tin cans to provide iron (Catala, 1957; Small, 1972). Although there seems to be considerable scope for an expansion of banana and plantain pit cultivation, the taro beetle (Papuana sp.) may have caused widespread damage to plants grown in "pit plantations". When grown in villages, close to the lagoon side, mulching with organic material, coconut husks in particular, results in good yields.

The native fig or te bero (Ficus tinctoria) is commonly cultivated around villages and occasionally in plantation areas. Moul (1957:12) reported it as common around abandoned babai pits and present in small thickets in rich soils around Pisonia grandis groves on Onotoa atoll in southern Kiribati. It is propogated vegetatively by planting branch cuttings, its fruits being an important staple in the drier southern islands. The fruit are picked when ripe and sometimes when green, cooked, crushed in a mortar into a puree which can be eaten after being sweetened with toddy molasses (kamaimai) or sugar and grated coconut or preserved by drying in the sun on Guettarda speciosa leaves. It reportedly bears many times throughout the year, and has wide cultural utility (Table Z)(Luomala, 1953; Catala, 1957; Small, 1972).

The common fig or te biku, reportedly introduced by missionaries, seems to be very well adapted to the atoll environment and is occasionally found propogated by cuttings in village home gardens.

The lime (Citrus aurantiifolia) is by far the most common citrus fruit grown in Kiribati, but is found only occasionally in villages. The fruit is highly sought after for squeezing on fish and other foods and for making drinks. Lemon trees are present on the agricultural experiment farm at Bikenibeu, but rare elsewhere.

Other Cultivated Food Plants

Other cultivated but minor tree-like food plants include sugarcane (Saccharum officinarum) and hibiscus spinach (Hibiscus manihot), which are both found only occasionally in villages around homes. Although sugarcane grows poorly in some localities, it shows promise where well mulched. Hibiscus spinach, a very nutritious green vegetable, reportedly introduced by contract workers returning from the phosphate mines on Banaba (Ocean Island), grows particularly well and shows little or no evidence of the insect or disease damage so characteristic in Fiji.

Giant Swamp Taro or Te Babai (Cyrtosperma chamissonis)

The major understory non-tree food plant in Kiribati is the ceremonially important staple, giant swamp taro or te babai (Cyrtosperma chamissonis), which is cultivated in pits excavated to the freshwater lens, using a very labour-intensive system of mulching. About 20 named cutivars are recognized (Small, 1982). Te babai is not a woody species, but because of the very sophisticated system of mulching and fertilization with leaves from numerous tree species, and because the babai pits are found within a matrix of coconut palms and other trees, te babai must be seen as an integral component of the Kiribati agroforestry system.

Te babai was probably more extensively cultivated in the past, as evidenced by the numerous abandoned pits, some of which have been overrun with coconut seedling and weeds. Although pits are often abandoned due to increasing brackishness, many were obviously abandoned long ago, with most pits being very ancient, the inhabitants having no recollection of their origin (Catala, 1957:68). On Abemama, for example, Watters and Banibati (1977:37) found, in a survey of 16 households, that whereas the mean number of pits in use was only 4.2, the mean number of empty pits per household was 23.4, with only 7.7 still containing the water necessary to produce te babai. Moreover, few of the productive pits were fully stocked, thus "reflecting more basically the changing food preferences and habits and growing reliance on the cash component of a household's total income" (Watters and Banibati, 1977:38). On Onotoa, Moul (1957:5) found that as many as ten individuals had separate plots in single pits ranging from 25 to 30 feet long and 10 to 20 feet wide.

As a result, te babai has become almost a luxury in many areas, reserved almost exclusively for ceremonial purposes, rather than constituting a staple food (Catala, 1957:67). Nevertheless, te babai cultivation continues to be surrounded with tradition, and there has been some recent rehabilitation of abandoned pits on both Tarawa and Abemama. As Catala (1957:67) relates: "pulling up a babai in order to offer the tuber to a distinguished guest is considered the greatest honour that can be paid to him."

Te babai pits must be excavated through as much as 1.5m of hard conglomerate and limestone to reach the freshwater lens, with Moul (1957:5) reporting pits up to 15 feet deep. The young shoots are planted in holes about 0.3m (2 feet) deep in the bottom of the pit and mulched and fertilized with black topsoil (te bon, te iarauri, or te ianuri) from stands of Guettarda speciosa, Scaevola sericea, and other plants and a variety of leaves, some of which are specially prepared for the purpose, using techniques generally not divulged. Baskets of pandanus or coconut leaves are commonly made, into which the shoot is planted or in which the fertilizer or mulch is administered to the plants in the pit.

Leaves used for fertilization and mulching, in order of importance, are te kaura (Sida fallax), te uri (Guettarda speciosa), te ren (Tournefortia argentea), te mai or breadfruit (Artocarpus spp.), te wao (Boerhavia repens), and to a lesser extent, species such as te kaura ni Banaba (Wollastonia biflora), te kanawa (Cordia subcordata), te kiaou (Triumfetta procumbens), and te kiaiai or te rao (Hibiscus tiliaceus). These leaves, with the exception of Sida fallax, are mixed with other plant waste, particularly old pandanus leaves and coconut refuse, black topsoil, and occasionally ground pumice (te uuan), and applied green or dried to the basket surrounding the plant or placed in the pit near the plant.

In the case of te kaura (Sida fallax), the leaves are rarely placed in the pits before drying, as their fermentation is believed to produce heat which can either kill or harm the te babai. The leaves are generally dried in the sun on mats and then taken to the pits in baskets, commonly mixed with other leaves, black top soil, and sometimes pumice; the mixture is then stirred to inhibit the formation of mould. The most

preferred topsoil is that found under te uri (Guettarda speciosa) trees (Catala, 1957:69-70; Small, 1972:68-69). As can be seen, the leaves of a variety of trees and the black topsoil found under trees are very important in te babai cultivation, and increasing agrodeforestation may be, at least in part, responsible for the decline in its cultivation in Kiribati.

Cultivated Exotic Timber Trees

Two trees deliberately introduced for reforestation purposes are the casuarina (Casuarina equisetifolia) and leucaena (Leucaena leucocephala). Casuarina, in particular, which was rare in the 1950s, has been widely planted on Tarawa as part of government sponsored reforestation programmes to provide windbreaks for recently planted coconut palms on the ocean sides of atoll islets (Overy et al., 1982:14) and to provide firewood. Leucaena was also introduced for reforestation purposes, because of its nitrogen-fixing ability, but is not widely planted.

Cultivated Ornamentals

Commonly cultivated ornamentals, most of which are found in houseyard gardens, mission settlements, schoolgrounds, or in major settlements, include plumeria or frangipani (Plumeria rubra and P. obtusa), hedge panax (Polyscias guilfoylei and P. fruticosa), copperleaf, Jacob's coat or the beefsteak plant (Acalypha amentacea), false eranthemum (Pseuderanthemum carruthersii), golden bells or yellow elder (Tecoma stans), bougainvillea (Bougainvillea spp.), lantana (Lantana camara), hibiscus (Hibiscus rosa-sinensis), dracaena (Dracaena fragrans), ixora (Ixora casei), and the poinciana or flame tree (Delonix regia). Also present in houseyard gardens, but not common, are the Tahitian gardenia (Gardenia taitensis), Acacia farnesiana, Cordyline fruticosa, and the Pacific fan palm (Prichardia pacifica). With the possible exceptions of Dracaena fragrans and Prichardia pacifica, all of these plants constitute important sources of flowers and leaves, which are used along with flowers from native species such as Guettarda speciosa, Sida fallax, and Scaevola sericea, used in the ubiquitous leis and head garlands so important for all social and ceremonial occasions (Table 2).

Important Indigenous Species

Important indigenous trees or tree-like species, which are integral and widespread components of the Kiribati agroforestry system include Scaevola sericea, Guettarda speciosa, Tournefortia argentea, Sida fallax, Morinda citrifolia, Clerodendrum inerme, Premna serratifolia, Pemphis acidula, and Dodonea viscosa (Table 2). Other indigenous trees, which are uncommon to rare in agricultural areas, but sometinmes found in coastal strand forest, houseyard gardens and villages, and as street trees in the main settlements, include Calophyllum inophyllum, Cordia subcordata, Terminalia catappa, Pisonia grandis, Hibiscus tiliaceus, Terminalia samoensis, Barringtonia asiatica, Hernandia nymphaeaefolia, Macaranga carolinensis, and Thespesia populnea. Also of localized importance are the mangrove species Rhizophora mucronata, Bruguiera gymnorhiza, and Lumnitzera littorea. All of these species have important cultural uses, many of which are described below and in Table 2. The information is based on in-the-field surveys and on Luomala (1953), Catala (1957), Moul (1957), and Overy et al., (1982).

Te mao (Scaevola sericea) is the most common shrub and the commonest understroy species and thicket former in Kiribati (Moul, 1957:22). It is found everywhere in coastal littoral forest, is common in plantations, especially where coconut density is low, and occasional in houseyard gardens and in villages and other habitats. It is an important

component of the coastal strand vegetation which provides protection from salt spray to inland plantations and gardens, is an important producer of humus and organic material because of its abundance, and has a wide ranging of cultural utility (Table 2).

Te Uri (Guettarda speciosa), te ren (Tournefortia argentea), and te kaura (Sida fallax), are the most common sources of leaf compost for the cultivation of te babai. Guettarda speciosa, one of the main components of the atoll vegetation, is occasionally cultivated in village gardens and particularly common in the centre of islets, where it is important in the formation of black topsoil te bon (te iarauri, or te ianuri) which is mixed with leaf-compost used in planting babai, pandanus trees and other crops. Its wood is used in general construction, its leaves are one the most important composts or fertilisers for babai, and its flowers are used in the production of garlands and head wreaths. All pastes or preserves are spread on its leaves for sun-drying, it is prominant in I-Kiribati legends, mythology, and is associated with phases of the moon and stations of the sun. It is easily one of the most culturally important plants in Kiribati (Table 2).

Te ren (Tournefortia argentea) is commonly found scattered in groups in plantation areas, occasionally in strips of ocean or lagoon strand forest, and was reported by Moul (1957:20) to be very common on the edges of babai pits on Onotoa. Like Guettarda speciosa, it has wide cultural utility. Its wood was occasionally used as a substitute for Calophyllum inophyllum for canoe bows and y-shaped pieces as spar supports on outrigger canoes. It also provides a favoured fuel, and was used as the bottom piece in making fire by friction in the past. The leaves are reportedly eaten in salads by boat crews, and used medicinally to reduce fever, as a female deodorant, and for magic and scenting coconut oil, as well as being an important ingredient in compost or fertiliser for babai and other plants. Te ren also features in many I-Kiribati legends.

Te kaura (Sida fallax), a small shrub found scattered throughout plantations, is occasionally in villages, and common on lagoon sides and on the inner margins of coastal ramparts of islands. It is a favored species for personal ornamentation, magic, particularly love magic, and is used medicinally. Its flowers and leaves are shredded and dried to produce the "strongest" compost or fertilizer for babai. Also occasional in plantation areas and cultivated as a living hedge or ornamental in home gardens is Clerodendrum inerme. It is reportedly used medicinally and its flowers used in garlands.

Te ngea (Pemphis acidula) is very common on sandy areas inland from mangroves and in clusters in garden areas bordering the ocean coast and on beach ramparts, where it often forms almost pure stands and serves as protection against sea spray. It is important medicinally, and the dense, extremely hard wood has wide utility, because of its resistance to sea water, and is a favoured firewood. Te kaiboia (Dodonea viscosa), indigenous to many Pacific islands, but possibly a recent introduction to Kiribati, locally common near existing villages and in sites of former dwellings and occasionally in garden areas, also has a variety of uses (Table 2).

Te non (Morinda citrifolia) and te ango (Premna serratifolia), two of the most important medicinal and magical plants in Kiribati, are occasional in coastal areas and relatively common in bush gardens and houseyard gardens in villages (Table 2). The pungent ripe fruit of M. citrifolia are occasionally eaten after boiling by old people, as a famine food , and as a stimulant on long fishing trips or ocean voyages, and the consumption of the young leaves has been actively promoted recently as a rich source of vitamin-A to combat outbreaks of vitamin A-deficiency night blindness among children.

Other indigenous species of wide cultural utility occasionally present in the coastal strand forest bordering garden areas, in houseyard gardens, or in settlement areas

include Calophyllum inophyllum, Cordia subcordata, Terminalia catappa, Pisonia grandis, Hibiscus tiliaceus, Terminalia samoensis, Barringtonia asiatica, Hernandia nymphaeaefolia, Macaranga carolinensis, and Thespesia populnea. All of these culturally useful species were more widespread in the past before official government emphasis was placed on clearing indigenous species to extend and rehabilitate coconut plantations and before current high population densities placed such pressure on limited arboreal resources.

Te kanawa (Cordia subcordata) is occasional in coastal forests and in villages, its attractive wood being highly valued for woodwork, and the inner bark, leaves, and attractive orange flowers highly valued for medicine, magic, composts and, garlands. Te kanawa is also featured in Kiribati legends and is the totem of the Karongoa clan.

Te kunikun (Terminalia catappa) and the related species, te ukin (Terminalia samoensis), both useful trees, are occasional in villages and in tree groves in plantations and inland from coastal littoral forest, almost always as individual trees, and sometimes planted as ornamentals. T. catappa is the favourite tree of the ancestral goddess Nei Tituaabane, and its mature seeds from the fruit (te ntarine) are eaten.

Te itai (Calophyllum inophyllum), so important medicinally and for general construction, canoe building and woodworking, is occasional around villages and towns, and was a sacred tree in the past on Tabiteuea.

Te buka (Pisonia grandis), the favoured nesting tree for the black noddy, an important food resource, is uncommon to occasional as isolated individuals or small groups, and has been recently planted in villages and at the hospital in Bikenibeu for its edible leaves, which are rich in vitamin A. It was probably more common in the past as a dominant in the indigenous climax forest. There reportedly remains a large traditional Pisonia reserve on the island of Onotoa in south Kiribati, which is surrounded by extensive guano deposits and the most luxuriant vegetation seen on the atoll (Moul, 1957:4).

The remaining species, te kiaiai or te rao (Hibiscus tiliaceus), te baireati (Barringtonia asiatica), te nimareburebu (Hernandia nymphaeaefolia), te nimatore (Macaranga carolinensis), and te bingiging (?)(Thespesia populnea) are all uncommon to rare in coastal strand forests, plantation areas, and villages on Tarawa and Abemama, despite their widespread cultural importance, often as babai compost. This, as suggested above, is probably the result of their widespread removal from coastal strand forests and the expansion of coconut monoculture in inland plantation and garden areas, coupled with the declining importance of the subsistence economy (Table 2).

The mangrove species serve as habitats and/or an important food supply for a majority of the important edible fish species. They also have an important role in coastal stability, land reclamation, and the protection of gardens from saltwater spray at the interface between the lagoon and agricultural areas. On Onotoa, they reportedly encircle nutritionally important fishponds (Moul, 1957:5). Mangroves are also used in construction and in the production of medicines, dyes and garlands (Table 2). They must, consequently, be considered integral components of agroforestry systems, particularly in land-scarce areas such as Kiribati. Te tongo (Rhizophora mucronata) is the most common species, forming very dense stands on swampy lagoon shores as well as being found on the the windward ocean coast at Bairiki, Tarawa. Te tongo or te buangi (Bruguiera gymnorhiza), is common to occasional in mangrove areas, and te aitoa (Lumnitzera littorea), although rare on Tarawa and possibly absent on Abemama, with only one large tree seen in Eita Village Tarawa, is reportedly more common on Butaritari.

POLYCULTURAL AGROFORESTRY AS AS BASIS FOR INNOVATION AND STABILITY

In summary, the 56 trees or tree-like species found in the agroforestry systems of Tarawa and Abemama represent a resource of enormous economic, cultural and ecological importance. These species, which along with the many other non-tree species have been preserved as part of the integral agroforestry system for generations, are now almost totally neglected by most agricultural developers and researchers. Consequently, although the agroforestry systems of Kiribati remain relatively in-tact on some islands, the push to encourage cash cropping of coconuts and small-scale commercial livestock production, and increasing urbanization have led to increasing agrodeforestation and neglect of many of these important tree species by a new generation of I-Kiribati who have become increasingly cash-oriented, and less tree-oriented, having not been educated to see the long-term utility of trees. Many young Kiribati, in fact, no longer know the local names nor the uses of these resources which made their ancestors self-sufficient.

As argued by Thaman and Clarke (1987), trees are both a symbol and a basis of stability in agroecosystems and will continue to be a precondition for sustainable development in the Pacific. Their very disadvantages as seen by modern developers (e.g., taking up space, lag-time between planting and maturity, perceived slow growth rates, etc.), which have often led to their domination or replacement by more immediately productive annuals, should be seen as advantageous in a world where biological stability is increasingly precarious. The "frozen" quality of trees - once established they are awkward to replace with other species - and the related lack of a quick turnover of product or landuse provide a permanence in ecosystems that slows misuse and provides a wide range of ecological benefits: diversity of habitat, diversity of species, prevention of accelerated erosion, maintenance of soil fertility and arable soil structure, flood retardation or prevention, and wind protection.

The culinary, nutritional, and medicinal value of trees and their contribution to dietary diversity and sustainable food, nutrition, and health-oriented development must be stressed in the light of the rapidly declining quality of nutrition and nutrition-related human health in the Pacific, a decline that has been widely documented, and which has led to very high incidences of nutritional disorders such as iron-deficiency anaemia, obesity, and general micro-nutrient deficiency and of nutrition-related non-communicable diseases such as cardiovascular disease, hypertension, diabetes, various forms of cancer, hyperuricaemia and gout, dental disease, and alcoholism (Coyne, 1984; Thaman, 1979, 1982b, 1983, 1985). Trends are similar in Kiribati and seem to be directly related to a decline in the consumption of traditional foods, which derive from the existing agroforestry system, such as toddy, coconut, breadfruit, pandanus, giant swamp taro and fish and a corresponding increase in the consumption of nutrient and fibre-depleted highly-processed imported foods (Wilmott, 1968; Pargeter et al., 1984).

With increasing population and urbanization and the almost exclusive official emphasis on monocultural production for export, and the associated growing neglect of traditional agroforestry-based food systems, there is also increasing food scarcity, both physical and economic (in terms of high prices), especially for the highly nutritious local staple food crops, fruit, and vegetables, and animal and fish protein, not to mention, dangerously high, and increasing levels of food dependency. Moreover, further agrodeforestation can only serve to create other destabilising dependencies on foreign sources for fuel, fertilizer, medicines, perfumes, and other material goods currently produced by existing agroecosystems. Similarly, ingenious and time-tested strategies for wild food acquisition, food processing, storage, and preservation have been all but

forgotten by many of today's youth and are in danger of disappearing (Massal and Barrau, 1956; Barrau, 1958, 1961; Yen, 1980ab; Klee, 1980; Parkinson, 1982; Thaman, 1982b, 1985).

In addition to their immense cultural and economic value, trees also provide the benefits of: 1) low labour requirements for maintenance compared with annuals, 2) provision of the "insurance" of a reserve food supply, should annuals fail, and 3) in combination with annuals in a two-story structure, which constitutes a more intensified utilization of space, aggregate yields greater than many monocultures of annuals (Thaman and Clarke 1987).

Given their many advantages, in terms of ecological and cultural utility, nutritional diversity and sustainability, economic self-reliance, and ecosystem and cultural maintenance, polycultural agroforestry systems, such as those found in Kiribati, would seem to offer ideal bases for further development and innovation, rather than being ignored as anachronisms or obstacles to "modern" development. It has even been suggested that the promotion of "urban agroforestry" may be one of the most cost-effective means of solving problems associated with increasing urbanisation in the Pacific islands (Thaman, 1987a).

Although there is a continuing need for innovation and modification of existing systems based on both internally and externally-induced or inspired changes or the incorporation of new species and agroforestry strategies, such innovation has already taken place, and continues to take place in response to changing ecological conditions, increasing population pressure, changing societal aspirations, and exposure to new plant species and agroforestry technologies, both prior to and after the time of European contact. The polycultural systems that exist today <u>are</u> the evidence of the continued willingness of Pacific island agroforesters to make rational decisions to adapt their systems to changing environmental and social conditions and technological options (Thaman and Clarke, 1987). It is critical, however, that today's development planners and managerial elite recognise the need to <u>base</u> modern agricultural and forestry development on such proven traditional Pacific island agroforestry systems, and, as suggested before, to see that the planting and preservation of trees within the matrix of existing agricultural systems is of tantamount importance to the promotion of the more monocultural agricultural and forestry development currently fostered in Kiribati and elsewhere in the Pacific islands. Rather than encouraging thoughtless agrodeforestation and associated helplessness, dependency, and the destruction of a significant part of the Kiribati cultural heritage in the name of short-term national economic development objectives, it might be possible, using a more balanced polycultural agroforestry approach, to foster development and innovation which would protect trees, people and their agroforestry traditions and to promote economic self-reliance and cultural and ecological stability in the atoll nation of Kiribati.

Table 2. Important tree and tree-like species of agroforestry systems of Kiribati, based on 1984 field research on the islands of Tarawa and Abemama. Notes: 1) under "Vernacular Names", the first name(s) listed are the Kiribati name (s) and the second the English or other common non-Kiribati vernacular names; 2) the article <u>te</u>, which is almost always used before a noun, is seen as being an integral part of the name and is found before almost all plant names except those named after people, eg. <u>neikarairai</u> or in some cases where the name is a direct "Kiribatization" of a non-Kiribati name, e.g., <u>nambere</u> from the Fijian <u>na</u> <u>bele</u>; 3) the vowels are generally pronounced: a as in father; e as in a in fate, although sometimes as the e in ten; i as ee in see; o as o in note, or sometimes as o in Bonny or aw in awful; u as oo in boot; 4) consonants such as ng are pronounced as the ng in sing; b sometimes like an English b, sometimes like an English p, often a sound in between both, or even like a sound between a b and v; k is

pronounced hard, often sounding more like a g (e.g. Kiribati sounds more as if it should be spelled Giribas in English); r as an unrolled English r; t like a normal t before the vowels a, e, and o, with ti being pronounced si or tsi, and tu being pronounced too, soo, or tsoo (e.g. Kiritimati is pronounced like Christmas in English and katuru is pronounced as it it were kasooroo in English; and w like a w in English, but also as a bilabial in some cases.

Latin Name	Vernacular Names	Notes
Cocos nucifera	te ni; coconut palm	Very abundant throughout the islands along lagoons, around villages, in garden and copra plantation areas, and in littoral strand vegetation on ocean coasts; apart from isolated large emergent trees, the superdominant upper story vegetation under which all agroforestry activities are practiced; the most important plant in Kiribati; a number of cultivars recognised; a major and perhaps the major staple food source in terms of calories in most areas, the mature endosperm being prepared in a myriad of ways, the juice of green nuts being an important beverage, and the vitamin and mineral- and energy-rich sap from the flower spathe, toddy (karewe), an important daily dietary item, a syrup made from boiled toddy (kamaimai), carmelized toddy (kareberebe), and fermented alcoholic toddy (te manging); mesocarp and male and female flowers used to cure infantile diarrhoea and gingivitis respectively; wood, fronds, husks, and shells the major source of fuel in the fuel-scarce atoll environment; the trunk provides useful timber for all types of construction from small coconut storage houses (te okai) to large meeting houses (maneaba) for posts and thatch; husks used as mulching; fibres of the husk provide string and matting; leaflets used for thatching, baskets, hats, binding and decoration; midribs of leaflets used in brooms; shells used for toddy containers, cups, spoons and bottles; oil used for soap, skin oil, perfume, and cosmetics; most parts of the tree extremely useful, some other uses including medicines, sorcery, general construction and a range of other functions; copra the only source of agricultural export income on most islands is made from mature nuts.
Artocarpus altilis	te mai, te bukiraro; breadfruit	Commonly planted around villages and residences, along roads, and occasionally in inland plantations amongst coconut palms and carefully looked after, mulched, and fertilized with tin cans, ground pumice to provide iron and other micronutrients; reportedly scarce on more arid southern islands, but common to abundant, especially on Butaritari in the north; reportedy introduced in pre-European-cantact times form either Polynesia or the Marshall Islands; very important seasonal staple eaten in a variety of ways; important shade tree in villages; overripe fruit fed to pigs; seeds cooked and eaten; timber sometimes used in construction and canoe making; sap chewed as gum; juice of leaves used for earaches and the buds chewed and spat into sore eyes; shoots used as treatment for fish poisoning; leaves used for composting; a number of cultivars recognized, including te mai kora and te moti ni wae.
Artocarpus mariannensis	te mai, te maitarika; Marianas breadfruit	Occasional to common in breadfruit groves around villages; uses as for A. altilis

Artocarpus altilis x mariannensis	te mai, te keang, te ang ni Makin, hybrid breadfruit	Occasional in breadfruit groves around villages; uses same as for A. altilis
Pandanus tectorius	te kaina; pandanus, screwpine	Abundant on all islands, where important cultivars are planted near villages and in plantations, with wild varieties found, primarily in coastal strand vegetation; the ancestral tree, from which, according to mythology, the progenitors of the I-Kiribati came; cultivated trees individually owned and well looked after, with each village having its own named cultivars; there are reportedly almost 200 recognised cultivars; extremely useful plant; a very important staple food, the ripe fruit of which is eaten raw and prepared in many forms, the most important being a desiccated cake for long storage (te tuae), a coarse flour from the pounded fruit (te kabubu); timber and stilt roots used in house construction, for digging sticks, and play things; adventitious root tips used in treating boils and sores and as an anti-pyretic; leaves after treating, used in production of fine mats, baskets, hats, skirts, good quality thatch, and, in the past, sails; leaves also used to thatch baskets into which ceremonial giant swamp taro (babai) are planted and composted; old leaves used in composting; leaves also used as bandages, swaps, tobacco or cigarette wrappers, whistles, and ornamentation; flowers and fruit used in garlands and the male flower (te taba) for scenting coconut oil; roots provide floats for fishing nets, red dye and fibre
Scaevola sericea	te mao; native salt bush	The most abundant shrub in Kiribati; found everywhere in coastal littoral forest, common in plantations, especially where coconut density is low, and occasional in villages and other habititats; important component of the coastal strand vegetation which provides protection from salt water spray to inland plantations and gardens; important producer of humus and organic material because of its abundance; branches sometimes used for roofing strips; leaves boiled with women's grass skirts (riri) to make them durable; pith of large trees cut into strips and made into paper-like garlands or necklaces; flowers used in garlands; fruits used medicinally and in magic
Guettarda speciosa	te uri	Very common tree, one of the main components of the atoll vegetation and particularly common in the centre of islets, where it is important in the formation of black topsoil (te iarauri or te ianuri) which is mixed with leaf-compost used in planting babai, pandanus trees and other crops; wood used as rafters and wall frames in housing, for canoe hulls and ribs, and formerly for firemaking by friction; leaves used alone and with other leaves as one of the most important composts or fertilisers for babai and other important plants; all pastes or preserves spread on te uri leaves for sun-drying; very important in I-Kiribati legends and mythology; names of the leaf and the plant asoociated with phases of the moon and stations of the sun; flowers among the most popular for garlands and head wreaths
Tournefortia argentea	te ren; beach heliotrope	Very common tree as scattered groups of trees and occasionally in strips of ocean or lagoon strand forest; wood occasionally used as a substitue for Calophyllum inophyllum for

canoe bows and y-shaped pieces as spar supports on outrigger canoes; wood a favoured fuel and used as the bottom piece in making fire by friction; leaves reportedly eaten in salads by boat crews and used medicinally to reduce fever and as a female deodourant, for magic and scenting coconut oil, and magic; leaves important ingredient in compost or fertiliser for babai and other plants; tree featured in I-Kiribati legends

Sida fallax	te kaura, 'ilima (Hawaii)	Common shrub found throughout plantations and occasionally in villages, especially on lagoon sides of islands; flowers and leaves shredded and dried to produce the "strongest" compost or fertilizer for te babai; often used as fresh green compost on Arorae in the south of Kiribati; flowers very important for garlands and personal ornamentation, formerly reserved for persons of high rank; parts of the plant used medicinally, the juice of the stem for headaches and stomach aches, crushed leaves with coconut oil as a treatment for tropical ulcers, herpes, and mouth sores; flowers used in magic, particularly love magic
Carica papaya	te mwemweara, te babaia, papaya, pawpaw	Very common in villages, where they receive little care; when well-cared-for, produce fruits of very good flavour; hollow leaf stalks used by children as pea shooters and as siphons; juice from shoots applied to corneal ulcers and latex applied to sores and wounds; fruit one of only readily available sources of vitamins A and C and commonly eaten, especially by children and the elderly; also cooked green in coconut cream; occasionally sold to passing ships for twist tobacco in the past
Ficus tinctoria	te bero; native fig, Dyer's fig	Commonly cultivated and propogated vegetatively by planting branch cuttings around villages and occasionally in plantation areas; branches sometimes used in house construction, especially in roof framing; fibrous twigs used for cleaning teeth; roots used as scoopnet frames; leaves fed to pigs and sometimes used as babai compost; fruits an important staple in the drier southern islands being picked when ripe and sometimes when green, cooked, crushed in a pestle into a puree which can be eaten after being sweetened with toddy molasses (kamaimai) or sugar and grated coconut or preverved by drying in the sun on Guettarda speciosa leaves; reportedly bears many times throughout the year; considered a pauper's or famine food in many areas; fruit formerly used to dye hats, mats, etc.; young leaves used in treating boils and watery inner bark used in treating sore eyes
Morinda citrifolia	te non; beach mulberry	Occasional in coastal areas and relatively common in bush gardens and in villages; wood of larger trees occasionally used in house construction, particularly for roofing; red dye for colouring mats and plaited ware prepared with the inner root mixed with ash; small leaves used to treat measles, the over-ripe fruit for warts, the juice from the leaf for boils, the ripe and unripe fruit to relieve coughing, and the root with toddy as a mouthwash; pungent ripe fruit occasionally eaten after boiling by old people, as a famine food, and as a stimulant on long fishing trips or ocean voyages; fruit also use in magic for love and fishing; young leaves used recently as a rich source of vitamin-A to combat outbreaks of vitamin A-difficiency-induced night blindness among children

Pemphis acidula	te ngea	Very common on rocky substrates, inland from mangroves and in clusters in garden areas bordering the ocean coast, where it serves as protection against sea spray; the dense

extremely hard wood used for house frames, the tops of canoe masts, pestles, coconut huskers, axe handles, smoking pipes, war clubs, combs, moray eel traps, to attach the outrigger to canoes, and , in the past, fish hooks, because of its resistence to sea water; as firewood, it makes the hottest flame; rotting wood added to coconut oil as a cosmetic, young leaves said to have antiscorbutic properties, the roots, scraped in water to make a hemostatic drink for women to stop post-childbirth hemorrhaging and to treat sores; small fruits sometimes eaten

Premna serratifolia	te ango	Occasional on the lagoon sides of islands and in villages; wood used in house construction and for making fire by friction; straight saplings or branches used for fishing poles; roots

used to perfume coconut oil; leaves used medicinally to cure post-childbirth hemorrhage, sinusitis, severe headaches, and as a poulstice for painful limbs; leaves also used for arousing love; mixture of bark and coconut milk used to banish fear in marriage and with te kaura flowers (Sida fallax) to promote true love

Rhizophora mucronata	te tongo; mangrove	Common, forming very dense stands on swampy lagoon var. stylosa shores and reportedly also found on the the windward ocean coast at Bairiki, Tarawa; one of the main components

of mangrove forest, serving as protection for villages and gardens against coastal erosion and salt water spray; dense and extremely hard wood used in house construction, for threading coconut shells for shark rattles, making scoop nets, and as stakes for fish traps because it resists salt water and shipworm damage; red dye obtained from the roots; bark used to prefume coconut oil; parts used medicinally to treat sore throat and gums; caulking paste made in the past from boiled fruits

Bruguiera gymnorhiza	te tongo, te buangi; mangrove	Common to occasional in mangrove areas; wood used in house construction; red dye from bark used to preserve and colour canoe sails; bright red flowers used in garlands
Dodonea viscosa	te kaiboia; native hopbush	Locally common near existing villages and in sites of former dwellings and occasionally in garden areas; stems make good fishing rods and frames for scoopnets; fruit used in garlands; young leaves used to scent coconut oil
Plumeria rubra	te meria; frangipani, plumeria	Commonly cultivated ornamental in villages and around homes; flowers used in garlands for ceremonies and everyday use; sap from flower mixed with coconut oil and water to

treat sores and sore eyes, leaves used to treat stomach disorders in children

Polyscias guilfoylei	te toara; hedge panax	Commonly cultivated as a living hedge and ornamental in villages and around dwellings; fagrant leaves used in garlands; cooked young leaves reportedly fed to children as a source of vitamin A to inhibit the recent spread of vitamin A-deficiency-induced night blindness among children
Acalypha amentacea vars.	te aronga; copperleaf, beefsteak plant	Commonly cultivated ornamental in villages; planted as a hedge or living fence; leaves used in garlands
Musa ABB Group	te banana, te umuumu, plantain, cooking banana	Occasional in villages and in pits and reportedly more common on Butaritari in the north; planted and fertilised or composted with black soil form under Scaevola sericea and Guettarda speciosa trees in pits dug down to the water table and occasionally planted on the surface and heavily mulched and composted with leaves, tin cans, and coconut husks; fruit cooked as a supplementary staple; reportedly very susceptible to damage by the taro beetle (Papuana sp.)
Musa AAB Group	te banana, te oraora, lady's-finger banana	Occasional in villages and in pits and reportedly more common on Butaritari; planted as the above cultivar; ripe fruit eaten raw; reportedly susceptible to damage by the taro beetle (Papuana sp.)
Pseuderanthemum carruthersii vars.	te iaro; false eranthemum	Commonly cultivated ornamental in villages; branches used for fishing rods for small fish; flowers and leaves used in garlands
Tecoma stans	neikarairai; yellow elder, yellow bells	Commonly cultivated ornamental in villages; bright yellow flowers used in garlands
Bougainvillea spp.	te akanta; bougainvillea	Moderately common cultivated ornamental in villages; flowers used in garlands
Clerodendrum inerme	te inato	Commonly planted as a hedge or ornamental plant and occasional in plantations; leaves, bark and sap used medicinally; flowers used in garlands
Lantana camara	te kaibuaka; lantana	Occasionally cultivated ornamental in villages; flowers used in garlands and in hair; flowers reportedly used to treat infantile diarrhoea; ripe fruit reportedly eaten by children

Hibiscus rosa-sinensis	te roti; hibiscus	Occasionally cultivated in villages; flowers used for decoration in hair
Citrus aurantiifolia	te raim; lime	Occasionally planted in villages and home gardens; seems to grow well in the atoll environment; ripe fruit highly desired for marinating fish, squeezing on food, and for making drinks
Saccharum officinarum	te kai tioka; sugar	Occasionally cultivated in villages and in home gardens; seems to grow reasonably well in some areas; stem chewed as a snack food
Hibiscus manihot	nabere; hibiscus spinach	Occasionally cultivated around houses in villages; leaves cooked as a vitamin- and protein-rich spinach; grows particularly vigourously and disease-free in Betio, where it was supposedly introduced by contract workers returning fom Banaba (Ocean Island)
Ixora casei	te katiru, te katuru; ixora	Occasionally cultivated in villages; bright red flowers used in garlands
Cordia subcordata	te kanawa; sea trumpet	Occasional in coastal forests and in villages; reportedly more common in past in interior before coconut plantings were extended; attractive wood highly valued for canoes, especially for the key pieces of the bow and stern, for fishnet floats, tobacco pipes, and smaller saplings for fishing poles; inner bark used as pregnant woman's girdle to give magical protection; dry bark used in making fire; innerstem used medicinally as an astringent and cure for diarrhoea when mixed with rainwater, leaves used in treating fever and stomach disorder; leaves added to babai compost; attractive orange flowers highly valued for garlands; the te kanawa is the totem of the Karongoa clan and features in Kiribati legends
Terminalia catappa	te kunikun, te tarin, beach almond	Occasional in villages and in tree groves in plantations and inland from coastal littoral forest, almost always as individual trees; sometimes planted as an ornamental; reportedly very abundant on Banaba (Ocean Island) and formerly more abundant on Tarawa; wood used in house construction and for other purposes; mature seeds from fruit (te ntarine) eaten; leaves used for wrapping food for cooking in the earthen oven; desiccated pith of fruit used to rub corpses; favorite tree of the ancestral goddess Nei Tituaabane
Acacia farnesiana	te kai bakoa; klu	Occasionally cultivated ornamental in villages; fragrant aroma flowers used in garlands

Calophyllum inophyllum	te itai; Alexandrian laurel	Occasional around villages and towns, reportedly much more common in the past; a sacred tree in the past on Tabiteuea; wood used for bow pieces and ribs of canoes, canoe paddles, diving goggles, and in house construction; stems for scoopnet frames; tissues inside nut are crushed for the oil which is spread on sores; juice from the roots used to cure headaches; fruit also used medicinally for morning sickness, chicken-pox, and conjunctivitis; skin and outer flesh of fruit eaten; fragrant flowers used in garlands and to scent coconut oil
Ficus carica	te biku; common fig	Occasionally cultived and thriving in villages and around mission gardens; ripe fruit eaten
Pisonia grandis	te buka	Uncommon to occasional as isolated individuals or small groups, and, recently, planted in villages and at the hospital in Bikenibeu; probably more common in the past, as a dominant in the indigenous climax forest, and removed to make room for expansion of coconut plantings; planted as living bath house post providing shade and privacy; reportedly common in a native forest reserve in northern Onotoa and common in the bush and in villages in other islands; favoured nesting area for noddy terns, the black noddy being an important food resource; the soft wood used for canoe outriggers, for which it was highly valued, and the bottom piece in the fire plough to make fire by friction
Hibiscus tiliaceus	te kiaiai, te rau; beach hibiscus tree, beach mallow	Occasional around villages; probably more abundant in the past; wood used as the bottom stick in making fire by friction; branches sometimes used for outrigger booms; sprouts, when straight, make good fishing rods; fibres from inner bark sometimes uses to make skirts (riri); leaves used for compost and for wrapping food and for treating neurological disease
Casuarina equisetifolia	te katurina, te burukam; casuarina, ironwood, she oak	Increasingly common in villages and in reclaimed areas; introduced as a potential source of timber and fuelwood; occasionally used as fuelwood; useful as a windbreak on ocean side of islets to protect newly planted coconuts
Leucaena leucocephala	te kaitetua; leucaena	Occasional around government buildings and in settlements; introduced for reforestation as a leguminous plant for soil enrichment and firewood; not well established
Plumeria obtusa	te meria; frangipani, plumeria	Occasionally cultivated ornamental in villages and around homes; flowers used in garlands

Delonix regia	te tua; flame tree, poinciana	Occasionally cultivated ornamental in villages, especially in Betio; excellent shade tree; flowers used in garlands
Terminalia samoensis	te ukin	Uncommon in plantation tree groves and in villages; root used for treating mouth sores, part of plant used for treating coughing of blood; red fruit reportedly eaten by children and used in garlands
Barringtonia asiatica	te baireati; fish poison tree	Uncommon in villages, possibly planted from drift seeds; evidentally more common in the past; seed used as a fish supificant or poison
Hernandia nymphaeae-folia	te nimareburebu; lantern tree	Uncommon on the lagoon side of islands and occasionally around villages; wood used in house construction and for outrigger floats; possibly planted from drift seeds
Lumnitzera littorea	te aitoa	Uncommon large tree found in Eita Village Tarawa, but reportedly more common on Butaritari; bright red flowers used in garlands; wood used in house construction and in fish traps becuse of its durability in water; features in songs and legends
Macaranga carolinensis	te nimatore; macaranga	Rare large tree seen near Teorareke; one large tree at King George V school just destroyed; an endangered species in Kiribati
Gardenia taitensis	te tiare; Tahitian gardenia, tiare Tahiti	Uncommon cultivated ornamental in houseyard gardens; fragrant flowers used in garlands
Cordyline fruticosa	te rauti; ti plant	Uncommon cultivated ornamental in villages
Polysicias fruticosa	te kaimamara; hedge	Uncommon cultivated as an ornamental hedge plant in villages; leaves used in garlands
Prichardia pacifica	te bam; Pacific fan palm	Uncommon, but occasionally planted in villages as an ornamental
Psidium guava	te kuava; guava	Rare fruit tree at Bikenibeu; seems to grow welland offers potential for wider utilization; ripe fruit eaten

Thespesia populnea	te bingibing	Rare in coastal strand forest; reported from Butaritari; flowers used in garlands; leaves used in babai composts

Sources: Thaman, 1987; Luomala, 1953; Catala, 1957; Moul, 1957; Small, 1972; Overy et al., 1982; and in-the-field surveys.

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NO. 334

CORALS OF THE EASTERN RED SEA

BY

ARNFRIED ANTONIUS, GEORG SCHEER

AND CLAUDE BOUCHON

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CORALS OF THE EASTERN RED SEA*

BY

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ABSTRACT

Coral collections were made along the Saudi Arabian coastline of the Red Sea, from Haql in the north (Gulf of Aqaba), to Jizan in the south, including nearshore and offshore collecting sites. Corals were taken from all depth-zones in the Jeddah area (max. depth 65 m), but from shallow water only (max. depth 9 m) at all the other sites. The present collection consists of 146 species of Scleractinia, the octocoral *Tubipora musica*, and among hydrozoans 3 species of *Millepora*, and *Distichopora violacea*. 12 scleractinian species are new for the Red Sea: *Pocillopora cf.eydouxi, Acropora anthocercis, A. aspera, A. cerealis, A. divaricata, A. donei, A. echinata, A. monticulosa, Montipora peltiformis, M. turgescens, M. undata*, and *Porites australiensis*. Collections were made from 1981 through 1988.

INTRODUCTION

A substantial amount of literature is available on the exploration of the Red Sea, as shown by MERGNER (1984) and VINE & SCHMID (1987). In addition, as part of the Indian Ocean, the Red Sea was studied by ROSEN (1971), SCHEER (1984), and SHEPPARD (1987). Valuable papers on numerous aspects of the Red Sea are also contained in the Proceedings of the Mabahiss/John Murray Internat. Symp., edited by ANGEL (1984). Other studies include KLAUSEWITZ's (1964) work on fishes, and SCHEER & PILLAI's (1983) descriptions of corals and coral reefs. References to most of the existing literature on the Red Sea are contained in these contributions.

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*) *We dedicate this paper to the memory of the late Marie-Helene Sachet, a dear friend and admired colleague.*

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We, therefore, will present only a brief review of coral research along the east coast of the Red Sea. The first biological investigations were undertaken by Peter FORSKAL who reached Jeddah in 1762 with the Danish "Arabia Felix" expedition. Besides plants and fishes, he also collected corals. Although he died from malaria in 1763 in Yemen, 26 species of corals were sent back to Copenhagen and were described posthumously by NIEBUHR (1775), and restudied by CROSSLAND (1941).

In 1825, Ehrenberg and Hemprich passed Jeddah on their way farther south, in an expedition described by STRESEMANN (1954). While Hemprich also fell pray to malaria, Ehrenberg sent back to Berlin 376 specimens of 62 species of corals from Suez, El Tur, and the southern Gulf of Aqaba (EHRENBERG 1834).

KLUNZINGER, although he collected in Koseir, Egypt, should be mentioned here because of his three volume publication on corals (1879), and description of a coral reef (1872). In 1888, FAUROT reported on corals from the Yemeni island of Kamaran.

During two expeditions (1895/96 and 1897/98) of the Austrian research vessel "Pola", MARENZELLER collected corals along the east coast of the Red Sea around Jeddah (see also: SCHEER & PILLAI 1983: 14, Fig. 1), and published his results in 1906.

Although working on the west coast, CROSSLAND's numerous contributions from 1907 to 1939 are too important to be neglected. His main work (1952) covers both Red Sea and Australian corals.

During the "Calypso" expedition, NESTEROFF (1955) and GUILCHER (1955) studied coral reefs of the Farasan Bank. Coral species were determined by Pichon, but this list was not published.

HASS (1961) directed the second "Xarifa" expedition in 1957/58, exploring coral reefs and collecting corals throughout the Red Sea (SCHEER 1971), with special emphasis on corals from the Sarso Islands (SCHEER 1967).

The hydroid-fauna at Port Sudan, Suakin, and Jeddah was investigated by MERGNER (1967).

In addition, the German "Meteor" expedition in 1964/65 supported some biological studies around the Sarso islands, documented by GERLACH (1967), KLAUSEWITZ (1967), SCHEER (1967), and SCHAEFER (1969).

In 1967, the Israeli Marine Biological Laboratory was founded at Eilat and initiated a large number of coral studies, such as LOYA & SLOBODKIN (1971) and LOYA (1972).

Also the Jordanian Marine Science Station, established nearby at Aqaba in 1973, gave many visitors an opportunity to work on corals and coral reefs, e.g. MERGNER & SCHUHMACHER (1974, 1981), MERGNER & SVOBODA (1977), MERGNER (1979, 1981), and BOUCHON (1980), as well as PICHON, JAUBERT, BOUCHON, & PETRON (1979, unpublished report).

Other studies include KUEHLMANN's (1970) work on reefs of Port Sudan and Massaua, and later (1976) at Port Sudan and Al Hudaydah on the Yemeni coast. Corals from many different Red Sea locations were described by SCHEER & PILLAI (1983).

A general review of the Saudi Arabian coast and its biogeographic subzones was given by ORMOND, SHEPHERD, PRICE, & PITTS (1984 a, b), while management-related aspects of these reefs are dealt with in an IUCN report by WELLS (1985). Reefs of the Saudi Arabian coast are also discussed in SHEPPARD & SHEPPARD (1985) and SHEPPARD (1985), and corals from this area are included in his list of Indian Ocean corals (SHEPPARD 1987).

The stony corals from the Saudi Arabian Red Sea described in this paper, were collected over a period of time extending from 1981 through 1988. The initial study consisted of a documentation of the coral communities in the Jeddah area by C.Bouchon and A.Antonius in 1982/83. This was reported as an oral presentation (BOUCHON & ANTONIUS 1983), which described a substantial collection of corals from all depth-zones.

Further studies by Antonius all focussed on human impact or pathology on coral reefs, and the coral collections were made with these objectives in mind rather than aiming at comprehensiveness. Since most of the syndromes studied are shallow water phenomena, the majority of the collections consists of shallow-water corals.

Some of the human impact studies (ANTONIUS 1984a), and most of the pathology studies (e.g. ANTONIUS 1984b, 1985a, 1985b, 1988b) were carried out in the Jeddah area. Later projects, however, encompassed the entire length of the Red Sea (see chart) and yielded a rich harvest of the major shallow water reef-builders, such as *Acropora* species and others (ANTONIUS 1987, 1988a, 1988c).

THE RED SEA

The Red Sea, including the Gulf of Aqaba, is about 2,100 km long, with a maximum width of slightly over 300 km in the Farasan area, and extens down to depths of 2,600 m in the center off Jeddah, and 1,800 m in the Gulf of Aqaba. Thus, the Red Sea is a long and narrow, but deep water body (ANTONIUS 1988c).

Good water circulation (NEWMAN & McGILL 1962) and exchange with the Indian Ocean diminishes the effect of extremes, such as temperature and salinity, and creates a suitable environment for coral reef growth (ANTONIUS 1984a). This is further enhanced by the climate. Both coasts of the Red Sea exhibit arid or semi-arid characteristics, with the result that there are no rivers entering the Red Sea.

Thus, water pollution today is restricted to urban-industrial areas, such as Haql, Yanbu, and Jeddah, where desalination plants create an artificial influx of polluted freshwater, but along most other expanses of the coast, the environment seems relatively undisturbed (ANTONIUS 1988c). However, latest observations indicate that even these comparatively healthy reef areas are beginning to show the first signs of deterioration (ANTONIUS, unpublished).

Reefs are developed as an almost continuous line of fringing reefs along the coast, along with a system of offshore patch and bank reefs. The distribution of offshore reefs is largely controlled by the presence of shallow platforms ("continental" shelf), which are part of the relief formed by local block-faulting.

Substantial platforms with numerous patch and bank reefs are located just south of Al-Wajh and Yanbu, as well as just north of Jeddah (Eliza Shoals); they are up to about 30 km wide.

Both Qunfudah and Jizan are bordered by the huge Farasan Bank, which is about 100 km wide and 500 km long, with the largest of all islands, the Farasan group, in the south.

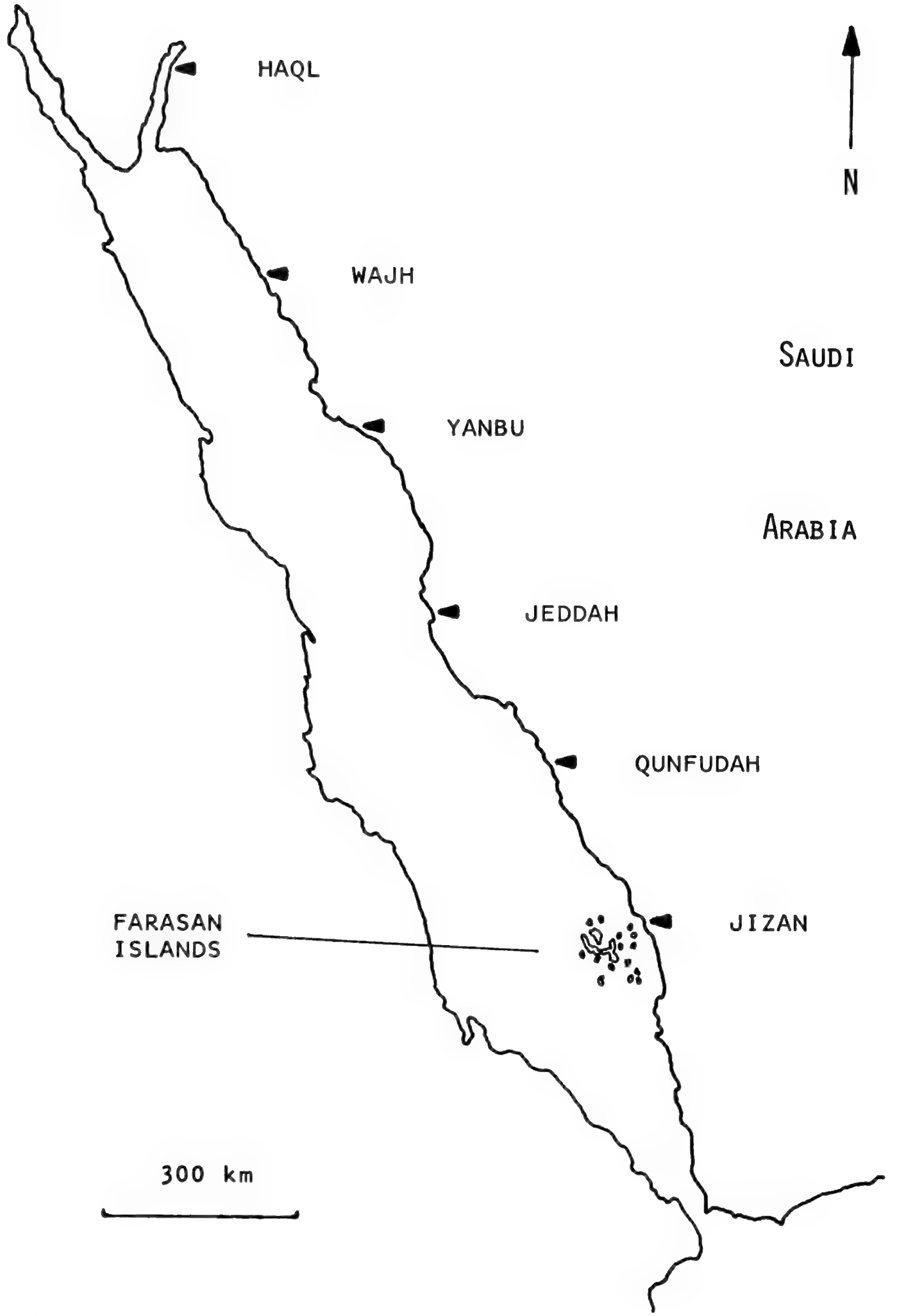

CHART of the Red Sea with the locations of the principal collecting sites in Saudi Arabia.

THE COLLECTING SITES

1) Haql

At Haql in the Gulf of Aqaba collections were made at three sites of the fringing reef, at locations a) Lat. 29° 19′ 40" N, Long. 34° 57′ 00" E, and 3.5 km N of Haql Coast Guard Harbor; b) Lat. 29° 17′ 24" N, Long. 34° 56′ 00" E, and 1.4 km W of Haql Coast Guard Harbor; c) Lat. 29° 16′ 55" N, Long. 34° 55′ 00" E, and 3.5 km SSW of Haql Coast Guard Harbor. The reef face drops off to a sandy slope, on an incline that continues down to the central depth of the Gulf.

Corals were collected at the reef edge and reef slope in depths of 0.5 - 3 m.

2) Al-Wajh

Collections were made along the fringing reef at the entrance of Sharm al-Wajh, which is also the fishing-boat harbor of the original village. The location is Lat. 26° 13′ 12" N, Long. 36° 27′ 14" E, and 400 m W of al-Wajh Harbor. The fringing reef drops off vertically to about 20 m, then grades into a slope that continues down to a depth of 200 - 300 m.

Corals were collected along the reef edge in shallow water, 1 - 3 m deep.

3) Muraykhah S

This is an atoll-like reef complex of considerable size (about 12 km longest diameter), bordered by 300 - 1000 m deep water. Collections were made along the seaward side of the reef barrier, the site located at Lat. 26° 10′ 26" N, Long. 36° 25′ 12" E, and 5.9 km SW of Sharm al-Wajh entrance.

Corals were collected from the upper part of the reef face, between water depths of 1 - 7 m.

4) Muraykhah L

The same reef comlex as No. 3, but collections were made at the lagoonward side of the barrier, located at Lat. 26° 10′ 18" N, Long. 36 ° 25′ 12" E, and 6.1 km SW of Sharm al-Wajh. The reef drops off to a 4 m deep, sandy lagoon floor.

Corals were collected along the edge of the reef barrier in shallow water, 0.3 - 2.5 m deep.

5) Yanbu

Collections were made at two patch reefs, one located at Lat. 23° 56′ 24" N, Long. 38° 12′ 36" E, and 1 km SW of King Fahad Port center, the other located at Lat. 23° 56′ 12" N, Long. 38° 11′ 18" E and 2.8 km SW of King Fahad Port center. The sides of both reefs drop off to a sandflat in about 20 m depth, but with deeper water (approx. 200 m) adjacent.

Corals were collected from the top and slope of both reefs in shallow water, 0.3 - 4 m deep.

6) Jeddah

The Jeddah collection came from numerous sites. Most of them were located on Eliza Shoals, a platform (about 20 m average depth, but with depressions and valleys of over 100 m depth in it) that is separated from the mainland by a 5 km wide and 400 m deep trough. The approximate center of the 20 km wide and 50 km long platform is located at Lat. 21° 45′ N, Long. 38° 58′ E, and about 40 km NW of Jeddah Islamic Port.

Another important collecting site was the fjord-like, 30 m deep Sharm Abhur, the entrance of which is located at Lat. 21° 42′ 20" N, Long. 39° 05′ 10" E, and 27 km NNW of Jeddah Islamic Port.

However, sporadic collections were made over an area spreading approximately 70 km to the N and 70 km to the S of Jeddah Islamic Port.

Corals were collected from the shallowest to the deepest parts of the reef zonation, comprising a depth range of 0.3 - 65 m.

7) Qunfudah

Collections were made at a nearshore bank reef called Jazirat as-Siqalah, located at Lat. 19° 04′ 5" N, Long. 41° 04′ 00" E, and 1.7 km SW of Qunfudah Port. The reef shows a large, very shallow top, with sides sloping off to a sand-bottom in 15 - 20 m depth.

Corals were collected from the edge of the reef and from the slope at a depth range of 1 - 6 m.

8) Jizan

Collections were made at a nearshore bank reef, located at 16° 54′ 25" N, long. 42° 31′ 55" E, and about 1 km NW of Jizan Port. The bank reef has a shallow crest on the seaward side, while the flat reef top gradually slopes to about 3 m depth landward. The reef rises up from a 5 - 7 m deep sand flat.

Corals were collected along the shallow ridge and at deeper parts of the reef top in depths of 0.5 - 3 m.

9) Habar

This is a relatively large, low sand island, surrounded by a wide, very shallow shelf area. Collections were made at widely scattered reef patches to the S of the island, located at Lat. 16° 53′ 10" N, Long. 42° 25′ 6" E, and 11 km E of Jizan Port. Patch reefs grow on a 1.5 - 2.5 m deep sand bottom.

Corals were collected from the top and sides of the patch reef area, at a depth range of 0.5 - 2 m.

10) Abu Shagur

This is a rocky cliff, home to many sea-birds, bordered by a shallow platform to the SW and a 60 m deep trough to the NE. Collections were made at a site located at Lat. 16° 55′ 30" N, Long. 42° 17′ 25" E, and 25 km WNW of Jizan Port.

Corals were collected on the NE slope of the island, throughout a depth range of 0.5 - 9 m.

SYSTEMATIC LIST OF SPECIES

Containing: Anthozoa, Zoantharia, Scleractinia: 15 families, 48 genera, 146 species. Anthozoa, Octocorallia, Stolonifera: 1 family, 1 genus, 1 species. Hydrozoa, Milleporina: 1 family, 1 genus, 3 spec. Hydrozoa, Stylasterina: 1 fam., 1 gen., 1 spec.

Column numbers 1 through 0 (= 10) represent the following collecting sites (described in detail in the preceding chapter):
1) Haql (fringing reef), 2) Al-Wajh (fringing reef), 3) Muraykhah S (seaward slope of barrier reef), 4) Muraykhah L (lagoonward side of barrier), 5) Yanbu (two patch reefs), 6) Jeddah (many fringing and patch reefs), 7) Qunfudah (bank reef), 8) Jizan (bank reef), 9) Habar (patch reef), 10) Abu Shagur (fringing reef slope).

Right column symbols:
plus sign (+) = represented in Scheer & Pillai 1983
minus sign (-) = not listed in Scheer & Pillai 1983
numbers 1 - 23 = numbered comments at end of list

Class Anthozoa EHRENBERG 1834
Subclass Zoantharia de BLAINVILLE 1830
Order Scleractinia BOURNE 1900
Suborder Astrocoeniina VAUGHAN & WELLS 1943
Family Astrocoeniidae KOBY 1890

Stylocoeniella guentheri (BASS.-SM.1890)	.....6....	+

Family Thamnasteriidae VAUGHAN & WELLS 1943

Psammocora contigua (ESPER 1795)	.....6.8..	+
Psammocora explanulata v.d.HORST 1922	.....6....	+
Psammocora haimeana M.EDW.& HAIME 1851	.....6....	+
Psammocora nierstraszi v.d.HORST 1921	.....6....	+
Psammocora profundacella GARDINER 1898	1....6....	+

Family Pocilloporidae GRAY 1842

Stylophora pistillata (ESPER 1795)	.2...6..9.	+
Stylophora subseriata (EHRENBERG 1834)	.....6....	+
Stylophora wellsi SCHEER 1964	1..4.6....	+
Seriatopora hystrix DANA 1846	...4.6....	+
Pocillopora damicornis (LINNAEUS 1758)	....56....	+

Pocillopora cf. eydouxi (M.EDW.& H.1860)	.....6....	-
Pocillopora verrucosa (ELLIS & SOL.1786)	.....6....	+

Family Acroporidae VERRILL 1902

Acropora anthocercis (BROOK 1893)	1.3.......	1
Acropora aspera (DANA 1846)	.....6....	-
Acropora austera (DANA 1846)	....5.....	-
Acropora cerealis (DANA 1846)	1.........	-
Acropora corymbosa (LAMARCK 1816)	....5.....	+
Acropora cytherea (DANA 1846)	1234..7...	2
Acropora danai (M.EDWARDS & HAIME 1860)	1...5.7...	-
Acropora digitifera (DANA 1846)	1.......9.	3
Acropora divaricata (DANA 1846)	1.34.....0	-
Acropora donei VERON & WALLACE 1984	1.........	-
Acropora echinata (DANA 1846)	.....6....	-
Acropora eurystoma (KLUNZINGER 1879)	12.456....	+
Acropora formosa (DANA 1846)	......7..0	-
Acropora forskalii (EHRENBERG 1834)	........9.	+
Acropora gemmifera (BROOK 1892)	...4.6....	4
Acropora granulosa (M.EDW.& HAIME 1860)	.....6....	+
Acropora haimei (M.EDWARDS & HAIME 1860)	.....6....	5
Acropora hemprichii (EHRENBERG 1834)	123.567...	+
Acropora humilis (DANA 1846)	..3.......	+
Acropora hyacinthus (DANA 1846)	...4.6....	+
Acropora intermedia (BROOK 1891)	.....6..9.	6
Acropora monticulosa (BRUEGGEMANN 1879)	......7...	-
Acropora nasuta (DANA 1846)	....5.....	+
Acropora nobilis (DANA 1846)	......7...	+
Acropora pharaonis (M.EDW.& HAIME 1860)	..345.....	+
Acropora polystoma (BROOK 1891)	..34.67...	-
Acropora scandens (KLUNZINGER 1879)	.....6....	7
Acropora secale (STUDER 1878)	1..4..7...	-
Acropora squarrosa (EHRENBERG 1834)	.....6....	+
Acropora valenciennesii (M.EDW.& H.1860)	0	+
Acropora valida (DANA 1846)	12.4..7.9.	8
Acropora vaughani WELLS 1954	....5.....	-
Astreopora myriophthalma (LAMARCK 1816)	.....6....	+
Montipora circumvallata (EHRENBERG 1834)	....5...9.	+
Montipora danae BERNARD 1897	.....6....	9
Montipora erythraea v.MARENZELLER 1906	.....6....	10
Montipora gracilis KLUNZINGER 1879	....5.....	+
Montipora informis BERNARD 1897	.....6....	-
Montipora monasteriata (FORSKAL 1775)	.....6....	+
Montipora peltiformis BERNARD 1897	.....6....	-
Montipora spongiosa (EHRENBERG 1834)	........9.	+
Montipora tuberculosa (LAMARCK 1816)	...4......	+
Montipora turgescens BERNARD 1897	.....6....	-
Montipora undata BERNARD 1897	........9.	-
Montipora verrucosa (LAMARCK 1816)	.....6....	+

Suborder Fungiina VERRILL 1865
Family Agariciidae Gray 1847

Pavona cactus (FORSKAL 1775)	.....6....	+
Pavona decussata (DANA 1846)	.....6..9.	+
Pavona diffluens LAMARCK 1816	.....6....	11
Pavona divaricata LAMARCK 1816	.....6....	+
Pavona explanulata (LAMARCK 1816)	.....6....	+
Pavona maldivensis (GARDINER 1905)	.....6....	+
Pavona varians VERRILL 1864	.....6.8..	+
Leptoseris explanata YABE & SUGIY.1941	.....6....	+
Leptoseris hawaiiensis VAUGHAN 1907	.....6....	+
Leptoseris mycetoseroides WELLS 1954	.....6....	+
Leptoseris tenuis v.d.HORST 1921	.....6....	+
Leptoseris yabei (PILLAI & SCHEER 1976)	.....6....	12
Gardinoseris planulata (DANA 1846)	.....6.8..	+
Pachyseris speciosa (DANA 1846)	.....6....	+

Family Siderastreidae VAUGHAN & WELLS 1943

Siderastrea savignyana M.EDW.& HAIM.1849	.....6....	+
Coscinaraea monile (FORSKAL 1775)	.....6....	+

Family Fungiidae DANA 1846

Cycloseris distorta (MICHELIN 1843)	.....6....	+
Cycloseris patelliformis (BOSCHMA 1923)	.....6....	+
Fungia danai MILNE EDWARDS & HAIME 1851	....5.....	+
Fungia fungites (LINNAEUS 1758)	.....6.8..	+
Fungia granulosa KLUNZINGER 1879	.....6....	+
Fungia horrida DANA 1846	.....6....	+
Fungia klunzingeri DOEDERLEIN 1901	.....6....	+
Fungia moluccensis v.d.HORST 1919	.....6....	+
Fungia paumotensis STUTCHBURY 1833	.....6....	13
Fungia repanda DANA 1846	.....6....	+
Fungia scruposa KLUNZINGER 1879	.....6....	+
Fungia scutaria LAMARCK 1801	....56....	+
Ctenactis echinata (PALLAS 1766)	....56....	14
Herpolitha limax (ESPER 1795)	....56....	+
Podobacia crustacea (PALLAS 1766)	.....6....	+

Family Poritidae GRAY 1846

Goniopora klunzingeri v.MARENZELLER 1906	.....6....	+

Goniopora planulata (EHRENBERG 1834)	.....6....	+
Goniopora savignyi DANA 1846	.....6....	+
Porites australiensis VAUGHAN 1918	1..4......	−
Porites lobata DANA 1846	1..4.67...	+
Porites lutea MILNE EDWARDS & HAIME 1851	1..4.6...0	+
Porites nodifera KLUNZINGER 1879	.......8..	+
Porites rus (FORSKAL 1775)	.2.4.6....	15
Porites solida (FORSKAL 1775)	1..4.6...0	+
Alveopora allingi HOFFMEISTER 1925	1.........	16
Alveopora verrilliana DANA 1872	.....6....	+

Suborder Faviina VAUGHAN & WELLS 1943
Family Faviidae GREGORY 1900

Favia favus (FORSKAL 1775)	1....6....	+
Favia laxa (KLUNZINGER 1879)	.2...6....	+
Favia pallida (DANA 1846)	1....6....	+
Favia stelligera (DANA 1846)	.2...6....	+
Favites abdita (ELLIS & SOLANDER 1786)	12...6....	+
Favites chinensis (VERRILL 1866)	.2...6....	17
Favites complanata (EHRENBERG 1834)	...4.6....	+
Favites flexuosa (DANA 1846)	12...6....	+
Favites pentagona (ESPER 1794)	.....6....	+
Favites peresi FAURE & PICHON 1978	.....6....	+
Goniastrea pectinata (EHRENBERG 1834)	1....6....	+
Goniastrea retiformis (LAMARCK 1816)	1...56..9.	+
Platygyra daedalea (ELLIS & SOLAND.1786)	.2...6..9.	+
Platygyra lamellina (EHRENBERG 1834)	.2...6....	18
Platygyra sinensis (M.EDW.& HAIME 1849)	.2...6....	+
Leptoria phrygia (ELLIS & SOLANDER 1786)	.....6....	+
Oulophyllia crispa (LAMARCK 1816)	.....6....	+
Hydnophora exesa (PALLAS 1766)	.....6....	+
Hydnophora microconos (LAMARCK 1816)	.....6....	+
Plesiastrea versipora (LAMARCK 1816)	.....6....	+
Montastrea annuligera (M.EDW.& HAI.1849)	.....6....	19
Montastrea curta (DANA 1846)	1.........	−
Diploastrea heliopora (LAMARCK 1816)	.....6....	+
Leptastrea bottae (M.EDWAR.& HAIME 1849)	.....6....	+
Leptastrea purpurea (DANA 1846)	.....6....	+
Leptastrea transversa KLUNZINGER 1879	1....6....	+

Cyphastrea microphthalma (LAMARCK 1816)	.2...6....	+
Cyphastrea serailia (FORSKAL 1775)	1....6....	+
Echinopora gemmacea (LAMARCK 1816)	12..56.8..	20

Family Oculinidae GRAY 1847

Galaxea fascicularis (LINNAEUS 1758)	.....6....	+

Family Merulinidae VERRILL 1866

Merulina ampliata (ELLIS & SOLAND. 1786)	.....6....	+

Family Mussidae ORTMANN 1890

Lobophyllia corymbosa (FORSKAL 1775)	.2...6....	+
Lobophyllia hemprichii (EHRENBERG 1834)	.....6....	+
Acanthastrea echinata (DANA 1846)	.....6....	+
Acanthastrea erythraea (KLUNZINGER 1879)	.....6....	21
Blastomussa merleti (WELLS 1961)	.....6....	+
Parascolymia vitiensis (BRUEGGEM. 1877)	.....6....	22

Family Pectinidae VAUGHAN & WELLS 1943

Echinophyllia aspera (ELL.& SOL. 1786)	.2...6....	+
Oxypora lacera (VERRILL 1864)	.....6....	+
Mycedium elephantotus (PALLAS 1766)	.....6....	+

Suborder Caryophylliina VAUGHAN & WELLS 1943
Family Caryophylliidae GRAY 1847

Plerogyra sinuosa (DANA 1846)	.....6....	+
Gyrosmilia interrupta (EHRENBERG 1834)	.....6....	+

Suborder Dendrophylliina VAUGHAN & WELLS 1943
Family Dendrophylliidae GRAY 1847

Tubastraea aurea (QUOY & GAIMARD 1833)	.....6....	+
Tubastraea coccinea (EHRENBERG 1834)	.....6....	+
Tubastraea micranthus (EHRENBERG 1834)	.....6....	+
Turbinaria mesenterina (LAMARCK 1816)	.....6.8..	+

Subclass Octocorallia HAECKEL 1866
Order Stolonifera HICKSON 1833
Family Tubiporidae EHRENBERG 1828

Tubipora musica LINNAEUS 1758	.2...6....	23

Class Hydrozoa OWEN 1843
Order Milleporina HICKSON 1901
Family Milleporidae FLEMING 1828

Millepora platyphylla EHRENBERG 1834	.....6....	-
Millepora exaesa FORSKAL 1775	........9.	-
Millepora dichotoma FORSKAL 1775	.....6....	23

Order Stylasterina HICKSON & ENGLAND 1905
Family Stylasteridae GRAY 1847

Distichopora violacea (PALLAS 1766)	...4.6....	23

Total: 2 classes, 2 subclasses, 4 orders, 5 suborders, 18 families, 51 genera, 151 species.

Numbers in the right column refer to the following:

1) in SCHEER & PILLAI 1983 as synonym of *A. eurystoma*
2) in SCH.& P. listed as synonym of *A. hyacinthus*
3) in SCH.& P. as synonym of *A. humilis*
4) in SCH.& P. as synonym of *A. humilis*
5) syn. with *A. yongei* n.sp. in VERON & WALLACE 1984
6) syn. with *A. nobilis* after VERON & WALLACE 1984
7) in SCH.& P. as synonym of *A. pharaonis*
8) in SCH.& P. as *A. variabilis* (KLUNZINGER 1879)
9) in SCH.& P. as syn. of *M. meandrina* (EHRENBERG 1834)
10) in SCH.& P. as synonym of *M. ehrenbergi* VERRILL 1872
11) ident. by HEAD 1980 as *P. cf. diffluens*
12) in SCH.& P. as *Pavona yabei*
13) in SCH.& P. only mentioned
14) same as *Herpetoglossa simplex* s. WELLS 1966
15) in SCH.& P. as *P. (Synarea) undulata* (KLUNZ. 1879)
16) in SCH.& P. as *A. mortenseni* CROSSLAND 1952
17) in SCH.& P. as *F. acuticollis* (ORTMANN 1889)
18) in SCH.& P. as synonym of *P. daedalea*
19) in SCH.& P. only mentioned
20) including the formae *fruticulosa* KLUNZINGER 1879, *hirsutissima* M.EDW.& H., and *mammillosa* KLUNZ. 1879 = *E. forskaliana* s. WIJSM.-BEST 1980
21) same as *Symphyllia erythraea* after HEAD 1980
22) only mentioned in SCH.& P.
23) not mentioned in SCH.& P., but described for the Red Sea in SCHEER 1967

DISCUSSION

Since this paper resulted mainly from studies on coral reef health in the Red Sea, it may be appropriate to briefly comment on the outcome of these investigations. As outlined in ANTONIUS (1988c), there are three problem areas among generally healthy reefs in the eastern Red Sea. In order of severity of impact they are: Jeddah, Yanbu, and Haql. But there is also a general slow deterioration over time noticeable at these sites, which appears to be spreading to healthy coral reef areas as well (ANTONIUS, unpublished). Mainly due to the increasing volume of oil-shipments in the Red Sea, this decline of environmental quality is bound to accelerate in the future.

Under these circumstances, it seemed prudent to systematically catalogue all the collected material. Fortunately, today the coral fauna of the Red Sea is still rich, as shown by the almost incidental coral harvest of this study.

The northernmost collecting site, Haql (site no. 1), is situated at the northern end of the Gulf of Aqaba, close to the Jordanian border. No corals were known from here. However, comparable collections exist from reefs near the Marine Science Station south of Aqaba in Jordan where MERGNER & SCHUHMACHER (1974: tables 6 and 13) studied a coastal fringing reef and a fringing reef with a lagoon. They found 60 and 48 species of scleractinians respectively, belonging to 30 and 28 genera. Later they could increase this number to 90 species and 36 genera (MERGNER & SCHUHMACHER 1981: tables 1 and 4).

PICHON, JAUBERT, BOUCHON & PETRON (1979) also collected in reefs south of Aqaba and documented their list of corals with 95 species of 46 genera in an unpublished research report of Nice University. Also comparable are the coral collections from Eilat, which were described by LOYA & SLOBODKIN (1971: table 1, 94 species of 38 genera), as well as SCHEER & PILLAI (1983: 101 species of 40 genera).

Among the corals collected at Haql are 5 species which are not contained in any of the lists mentioned, and also were not previously reported from any other part of the Red Sea. They are: *Acropora anthocercis* (site nos.1,3), *Acropora cerealis* (site no.1), *Acropora divaricata* (site nos.1,3,4,10), *Acropora donei* (site no.1), and *Porites australiensis* (site nos.1,4).

The three collecting sites at Al-Wajh (site nos.2,3,4) can be considered as one site. The closest locality from which corals were collected before is Sanafir Island, where v.MARENZELLER (1906) found 9 species of 6 genera. South of Al-Wajh, at Sharm Abban, he collected 14 species of 12 genera.

Among the Al-Wajh corals, three species are new for the Red Sea, *Acropora anthocercis*, *Acropora divaricata*, and *Porites australiensis*, which were also encountered at Haql.

At the next site, Yanbu (site no.5), SHEPPARD & SHEPPARD (1985: Appendix 2) found 104 scleractinian species of 47 genera, which SHEPPARD (1987: Appendix 1, list of coral species, column 3) increased to 133 species and 48 genera. The present collection contains 7 more species which were not previously reported from Yanbu, but from other parts of the Red Sea.

Corals from Jeddah (site no. 6) were reported by v.MARENZELLER (1906), who described 38 species of 18 genera. SHEPPARD (1985: table 2) also collected here, but his list of corals contains all samples from 27 sites along the entire Jeddah to Jizan coastline. While his table 2 lists 91 species of 45 genera, his fig.6 shows that 83 species were from Jeddah. This list was augmented by SHEPPARD (1987: Appendix 1, list of coral species, column 4) to 93 species.

The present, very large collection of corals from the Jeddah area (site no.6) comprises 116 scleractinian species of 47 genera, with the addition of 5 non-scleractinians from 3 genera (*Tubipora*, *Millepora*, *Distichopora*). The collection contains 5 species not known from any other location of the Red Sea, i.e. *Pocillopora cf. eydouxi*, *Acropora aspera*, *Acropora echinata*, *Montipora peltiformis*, and *Montipora turgescens*.

The next collecting site further south is Qunfudah (site no.7). From here, v.MARENZELLER (1906) brought back 3 species, but a short distance to the north, at Mamuret el Hamidije, he collected 18 species of 16 genera. SHEPPARD (1985: fig.6) reports 52 species from Qunfudah, but in his coral list does not specify which ones. The present collection contains 10 species of 2 genera, of which *Acropora monticulosa* has not previously been reported from the Red Sea.

The southernmost three collecting sites near Jizan (site nos.8, 9, 10) can again be combined. Together they yielded 23 species of 12 genera. New for the Red Sea is

Montipora undata, and *Acropora divaricata*, also found at Haql (site no.1) and Al-Wajh (site nos.3, 4). SHEPPARD (1985: fig. 6) collected 12 and 8 species respectively from two sites between Jizan and the Yemeni border, but without indicating which ones. Comparable collections were made at the Sarso Islands in front of Jizan. v.MARENZELLER (1906) published 9 species of 6 genera, and SCHEER (1967) 44 species of 20 genera, as well as *Tubipora, Millepora* (2 species), and *Distichopora*.

The present collection again shows how rich a coral fauna there is in the central Red Sea, but also in the Gulf of Aqaba. Toward the south, the number of species decreases significantly.

Twelve species listed here are new for the Red Sea: *Pocillopora cf. eydouxi* (site no.6); *Acropora anthocercis* (site nos.1,3); *Acropora aspera* (site no.6); *Acropora cerealis* (site no.1); *Acropora divaricata* (site nos.1,3,4,10); *Acropora donei* (site no.1); *Acropora echinata* (site no.6); *Acropora monticulosa* (site no.7); *Montipora peltiformis* (site no.6); *Montipora turgescens* (site no.6); *Montipora undata* (site no.9); and *Porites australiensis* (site nos.1,4).

From the Gulf of Aqaba (site no. 1) comes: *Alveopora allingi*.

Only in the central Red Sea (site nos. 5,6,7) occur: *Acropora vaughani; Montipora gracilis; Montipora informis; Pavona diffluens; Fungia repanda; Acanthastrea erythraea; Parascolymia vitiensis; Tubastraea coccinea.*

And exclusively in the southern Red Sea (site nos.8,9,10) were found: *Acropora valenciennesii*, and *Porites nodifera*.

While SCHEER & PILLAI (1983) described 180 species of 54 genera of hermatypic scleractinians from the Red Sea, SHEPPARD (1987: Appendix 1, list of coral spec. column 1) lists 221 species of 56 genera.

Now, 12 more species can be added, resulting in a total of 233 species of 56 genera of hermatypic Scleractinia from the Red Sea. Of these, 138 species (48 genera) are reported from the Gulf of Aqaba, 101 species (36 genera) from the northern Red Sea, 146 species (48 genera) from the central Red Sea, and 63 species (28 genera) from the southern Red Sea.

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THE WORLD-WIDE CORAL REEF BLEACHING CYCLE AND RELATED SOURCES OF CORAL MORTALITY

BY

ERNEST H. WILLIAMS, JR. AND LUCY BUNKLEY-WILLIAMS

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THE WORLD-WIDE CORAL REEF BLEACHING CYCLE AND RELATED SOURCES OF CORAL MORTALITY

BY

ERNEST H. WILLIAMS, JR. AND LUCY BUNKLEY-WILLIAMS*

ABSTRACT

World-wide "coral reef bleaching complexes" occurred in 1979-80, 1982-83 and 1986-88. Each included a "preceding event" 1 year (1979, 1982, 1986) before the most extensive ("main event") bleaching began. The 1986-88 complex also possessed a "following event" (1988). A number of minor bouts also occurred during each complex. Preceding events may be used to predict main bleaching events. We believe the world-wide coral reef bleaching complex "cycle" is caused by increased global temperatures of the 1980's. The progressive deterioration of inshore regions, including coral reefs, may have contributed to the intensity of the events. El Niño southern oscillation (ENSO) events of 1982-83 and 1986-88, on top of these problems, increased overall seawater temperatures, or provided conditions favoring increased inshore temperatures, to the levels necessary to bleach and kill coral reef photosymbiotic hosts. Decreased temperatures also caused minor bouts in 1988, 1989 and possibly other times. Deterioration of coral reefs has also lowered photosymbiotic hosts' resilience, or resistence to the bleaching process. Our model explaining coral reef bleaching employs increased global temperatures, increasing deterioration of reefs, and ENSO events. These conditions are not only well established, but seem almost certain to continue. The cycle may repeat in 1991 or 1992, possibly with more intensity, and will probably continue and increase until coral dominated reefs no longer exist.

INTRODUCTION

Coral reef bleaching has recently attracted considerable interest when spectacular and sudden bleaching occurred in 1987. This event led to a U. S. Senate Hearing (Hollings, 1988); Special Bleaching Sessions during scientific meetings in Mayaguez, Puerto Rico (November 1987), Curacao (November 1987), Sarasota, Florida (May 1988), Florida Keys (June 1988), San Salvador, Bahamas (June 1988), Townsville, Australia (August 1988), La Parguera, Puerto Rico (May 1989), and Havana, Cuba (June 1990); and a recent special volume by Brown (1989). In this paper, we describe the bleaching events of 1987-1988, a few previous bleaching occurrences which have not been published, and relate them to previously published reports of other bleaching events. We feel these events fall into patterns of world-wide bleaching complexes and further form a continuing cycle of bleaching. Our data set for 1986-1988 allows us to correlate conditions with events and bouts, to suggest a cause for the recent events, and, in combination with published accounts, to suggest an overall cause for the cycle. The escalation of deteriorating effects and signs of decline suggest an eventual loss of the coral reef system. A number of other major marine ecological disturbances require examination for common or related causes. The methods employed in our study and a proposed Alert and Communication Network are suggested as a practical means to follow these important, large-scale events.

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MATERIALS AND METHODS

We issued more than 1,000 copies of 2 summaries and 3 questionnaires (sample copy in Appendix 1) and wrote 694 individual letters. We received 271 reports from 159 people in 48 countries (as of 3 June 1989). Records were recorded as case reports of the Caribbean Aquatic Animal Health Project. We took information from scientists at face value. Reports by amateur scientists, who tended to be too cautious in their estimates and descriptions, have generally been corroborated by coral reef specialists in the same or similar regions. The original data from these letters and completed questionnaires (personal communications) forms the major part of this paper. Much of the cited material comes from recent unpublished reports, abstracts, newsletter articles and proceedings. To save space, the names, addresses and/or affiliations of people who provided information are listed in the Personal Communications (PC) section found after the References. Last names cited in the text, tables and figures with the term "PC" refer to this list. Second last names are abbreviated in the text, but spelled out in the Literature Cited or PC listing when known. For convenience in this paper the abreviation "sp." following a genus name will indicate 1 unidentified species in the genus and the term "spp." 2 or more unidentified species. This does not suggest that this usage is generally correct. The term "host" is used instead of "photosymbiotic host" to save space. Reference to species of cnidarians and sponges in this paper refer to colonies of each host. The terms "colony of" or "colonies of" have been ommitted in most cases to save space. Use of animal species names to designate these complex photosymbiotic associations is merely for convenience, not an attempt to ignore the nature of these relationships. Specimens deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, are designated with USNM numbers. A list of all species (in taxonomic order) used in this paper and their authors is included in Appendix 2. The description of the 1987-88 events are presented largely in tabular form to make this data more easy to follow (Tables 1-22).

DEFINITION OF TERMS

Many "bleaching" terms have been used in the past without adequate definition. We also employ some new combinations and new terms in this paper. For the purpose of clarity, the following definitions are provided:

BLACK BAND DISEASE (BBD): A cyanobacteria, *Phormidium corallyticum*, which invades Atlantic photosymbiotic hosts, possibly at points of damage, and inevitably destroys the entire colony. Disease progresses over stony coral heads in a circular pattern. The distinctive, narrow band of dark *P. corallyticum* filaments borders the remaining live coral leaving the white, bare skeleton in the center of the circle. Algae soon colonizes the bare skeleton (Ruetzler and Santavy, 1983; Peters, 1984). Ruetzler (1988) suggests that this pathogen may be a former cyanobacterial photosymbiont gone awry, similar to one he is studying in sponges. BBD or a similar condition also occurs in Indo-Pacific photosymbiotic hosts (Antonius, 1985). BBD has replaced "black line disease" as a term for this condition.

BLEACHING: Loss of photosymbiotic microorganisms (dinoflagellates, red and green algae, or cyanobacteria), or the pigments of these photosymbionts, or some of both, from tissues of host cnidarians, sponges, mollusks or other photosymbiotic host animals. The name comes from the whitening of many hosts which possess few pigments of their own. It replaces "blanching" (Jaap, 1985), "whitening" (Guillaume et al., 1983), etc. It should be accepted as a term and not placed in quotation marks.

CORAL(S): A common name for many anthozoans [octocorals (blue corals, soft corals, gorgonians), stony corals (also called "hard corals" or "true corals"), black corals] and hydrozoans (fire corals, stylaster corals). Often used incorrectly as a common name in place of stony corals or "hermatypic corals" (=stony, colonial, zooxanthellate photosymbiotic corals, with large skeletons, which form much of the living surfaces of coral reefs and the breakdown of their skeletal material provides much of the components for reef building).

CORAL REEF BLEACHING: A term suggested in place of "coral bleaching" because this condition is seldom limited to corals and most affected photosymbiotic hosts reside on coral reefs.

DIE-OFF: Death of more than 3, but fewer than 1000 individuals of animals or plants related in time, geographic area, and cause.

EPIZOOTIC: A disease temporarily prevalent among many animals of the same species. "Epidemic" applies only to humans, and should not be used to describe bleaching (Jaap, 1985) or diseases of corals (Williams and Williams, 1987).

MAJOR MARINE ECOLOGICAL DISTURBANCE: Mass mortality, epizootic or outbreak of organisms or conditions detrimental to biota affecting more than a few km^2 of area and occurring over more than a few days. Includes toxic red tides, fish kills, ciguatera outbreaks; but does not include direct effect of oil, toxic chemical, or radiation spills and/or contamination.

MASS MORTALITY: Death of 1000 or more individuals of animals or plants related in time, geographic area, and cause. Not interchangeable with "major marine ecological disturbance" or "epizootic".

PHOTOSYMBIOSIS: Photosynthetic mutualism between PHOTOSYMBIONTS (PHOTOSYMBIOTIC MICROORGANISMS) and PHOTOSYMBIOTIC HOSTS (see Bleaching definition). "Symbiont" was used incorrectly by Williams and Bunkley-W. (1989) as a term for both hosts and photosymbionts.

UNITS OF BLEACHING (Figure 1):

BOUT: The smallest portion of a bleaching disturbance which can be identified and separated in time.

EVENT: Made up of 1 or more bouts. An event is a period of continuous bleaching from the initial "outbreak" through final "recovery". Disturbances may vary slightly in time in different geographic locations and still be considered portions of the same event.

BLEACHING COMPLEX: A series of time-related bleaching events. Thus far, 2-3 events have made up a complex. Events in a complex may be recognized as "preceding", "main", and "following".

BLEACHING COMPLEX CYCLE: A complete round of bleaching, starting mid-way between complexes, through a complex and ending mid-way toward the next complex. Thus far, 1-2 years have separated complexes.

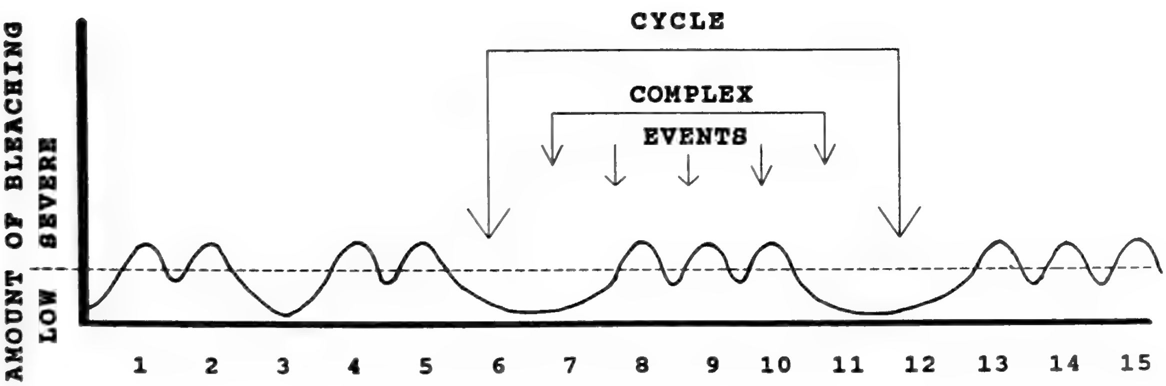


FIGURE 1. Diagrammatic Depiction of the Units of Bleaching.

WHITE BAND DISEASE (WBD): A disease of unconfirmed etiology, possibly due to adverse environmental conditions, with or without secondary bacterial infections, and/or due to a bacterial primary pathogen. WBD is characterized by sloughing of tissue starting from the base of the branches and progressing to the tips. Diseased corals may appear slightly lighter in color than normal. The disease may cease in some cases before an entire colony is destroyed. WBD or closely related conditions occur circumtropically in acroporids and other photosymbiotic hosts. The drastic decline of *Acropora* spp. in the tropical and subtropical Atlantic may be due to WBD, but almost all of these deaths have occurred in the absence of detailed examinations (Peters, 1984; Peters PC). WBD has replaced "white line disease" as a term for this condition. This disease and the related epizootics are in urgent need of definitive study.

ZOOXANTHELLAE: A common name for photosymbiotic dinoflagellates occurring in various marine hosts. Derived from names once proposed for generic taxa (Blank and Trench, 1986). Sometimes applied to photosymbionts other than dinoflagellates (loc. cit.), but we discourage such usage.

DESCRIPTION OF THE 1987-88 EVENTS

BEGINNING OF THE EVENT

Reports of mass loss of zooxanthellae from Florida, Mona Island, and Puerto Rico were noted by Williams and Bunkley-W. (1989). No similar reports were received from the Indo-Pacific or other parts of the Atlantic. The turbidity due to zooxanthellae in the otherwise clear waters of Puerto Rico and Mona Island indicated a relatively sudden and coordinated event. Reefs on the insular shelf edge (6.4 km offshore) and inshore reefs were intensely affected on the same day in Puerto Rico (Cintron PC).

A great variety in the speed of development of bleaching in different locations, different habitats and even at different times in the greater Caribbean area in 1987-88 was suggested by Williams and Bunkley-W. (1989) (Figs. 2,3). Since that paper, a report that bleaching developed suddenly in the Turks and Caicos (Lott PC) agrees with the original assessment of bleaching in that location by Spotte in Williams and Bunkley-W. (1989). In a closely monitored mangrove area in southwestern Puerto Rico, bleaching began suddenly in 1988 (and in 1986) (Perez-T. PC). In the Indo-Pacific, bleaching began slowly in the Gulf of California in 1987 (Reyes-B. PC) and in Hawaii in 1987 (and in 1986) (Choquette PC), but suddenly in Kenya (McClannhan PC) in 1987.

Only in areas where scientists were closely monitoring corals were details of the sequence of events in bleaching relative to depth available. We suspect that bleaching in most areas was noticed only after many preliminary depth developments were obscured. The limited records show oppos-

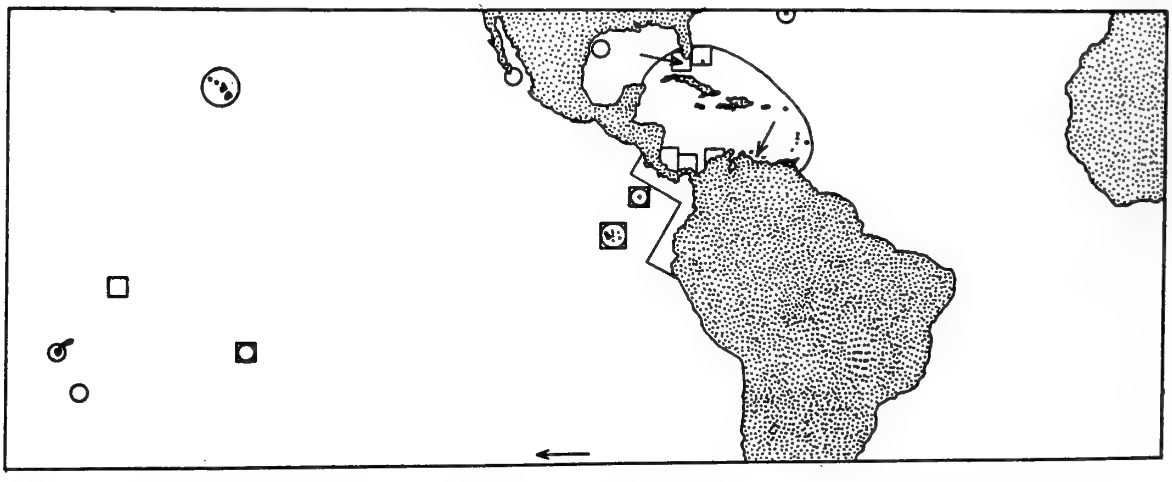


Figure 2: The world from 33°S to 33°N, Part 1: Central Pacific to Atlantic. 1979-80 Coral Reef (Part 1) Bleaching Sites Marked with Arrows, the 1982-83 with Squares and Rectangles, the 1986-88 in Circles and Elipses.

ing trends. In the Florida Keys and Puerto Rico, bleaching started in the shallows and moved deeper; in Jamaica and St. Croix, the opposite was observed (Williams and Bunkley-W., 1989).

Table 1: Photosymbiotic Hosts Which Bleached First.[1]

SPECIES	LOCATION	DATE	SOURCE
Acropora cervicornis	Culebra, Puerto Rico	1986	Perkins PC
	Looe Key, Florida	1987	Causey PC
Acropora palmata	Looe Key, Florida	1987	Causey PC
	Puerto Rico	1989	Lopez PC
Agaricia agaricites[2]	Puerto Rico	1986, 1987, 1988	Perez-T. PC
Agaricia lamarcki	St. Croix, USVI	1987	Gladfelter PC
Eunicia sp.	Turks and Caicos	1987	Lott PC
Millepora alcicornis	Puerto Rico	1987	Present paper
	Turks and Caicos	1987	Lott PC
Millepora complanata	Puerto Rico	1987	Present paper
	Turks and Caicos	1987	Lott PC
Palythoa caribbea[3]	Key Largo, Florida	1987	Hudson PC
	Looe Key, Florida	1988	Causey PC
Palythoa mammilosa	Bermuda	1988	Cook PC
Gorgonians	Teague Bay, St. Croix, USVI	1987	Gladfelter PC

[1]Williams and Bunkley W. (1989) listed 5 hosts that were first to bleach at 3 Caribbean locations.
[2]Especially sensitive to bleaching in the mangrove habitat.
[3]Gladfelter (PC) noted this host to frequently bleach. Causey (PC) considers it a bleaching "indicator organism". We have frequently noted it to bleach before and after the 1987 event.

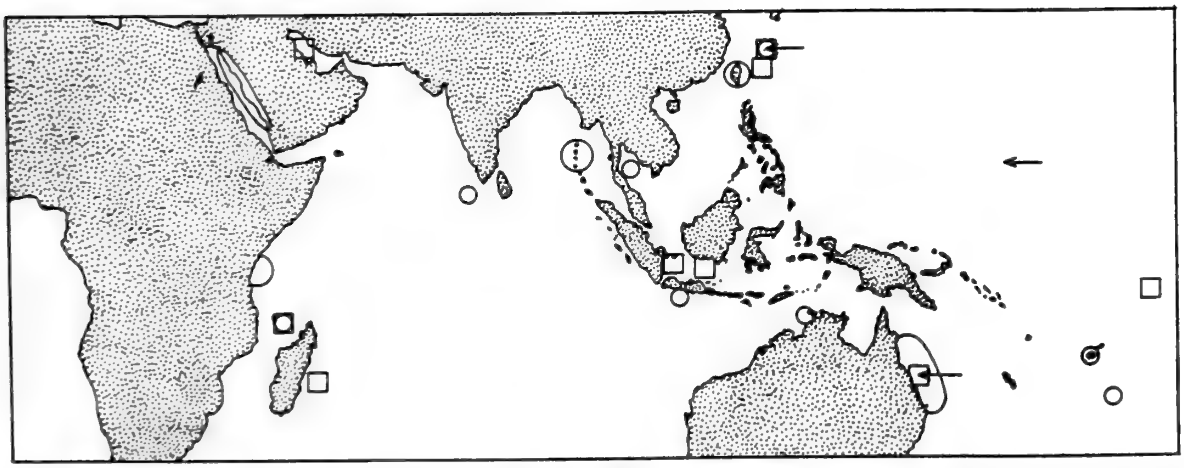
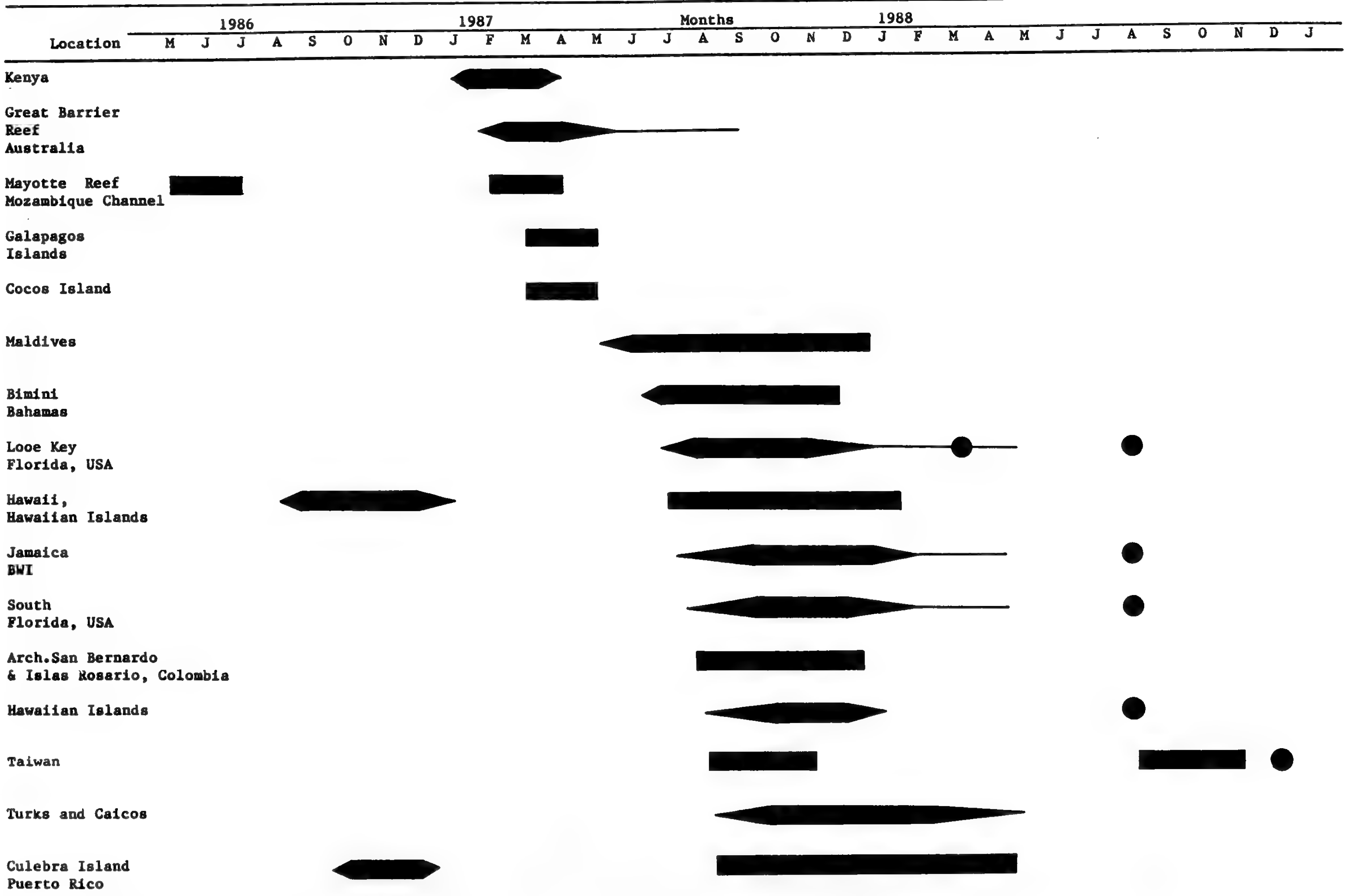
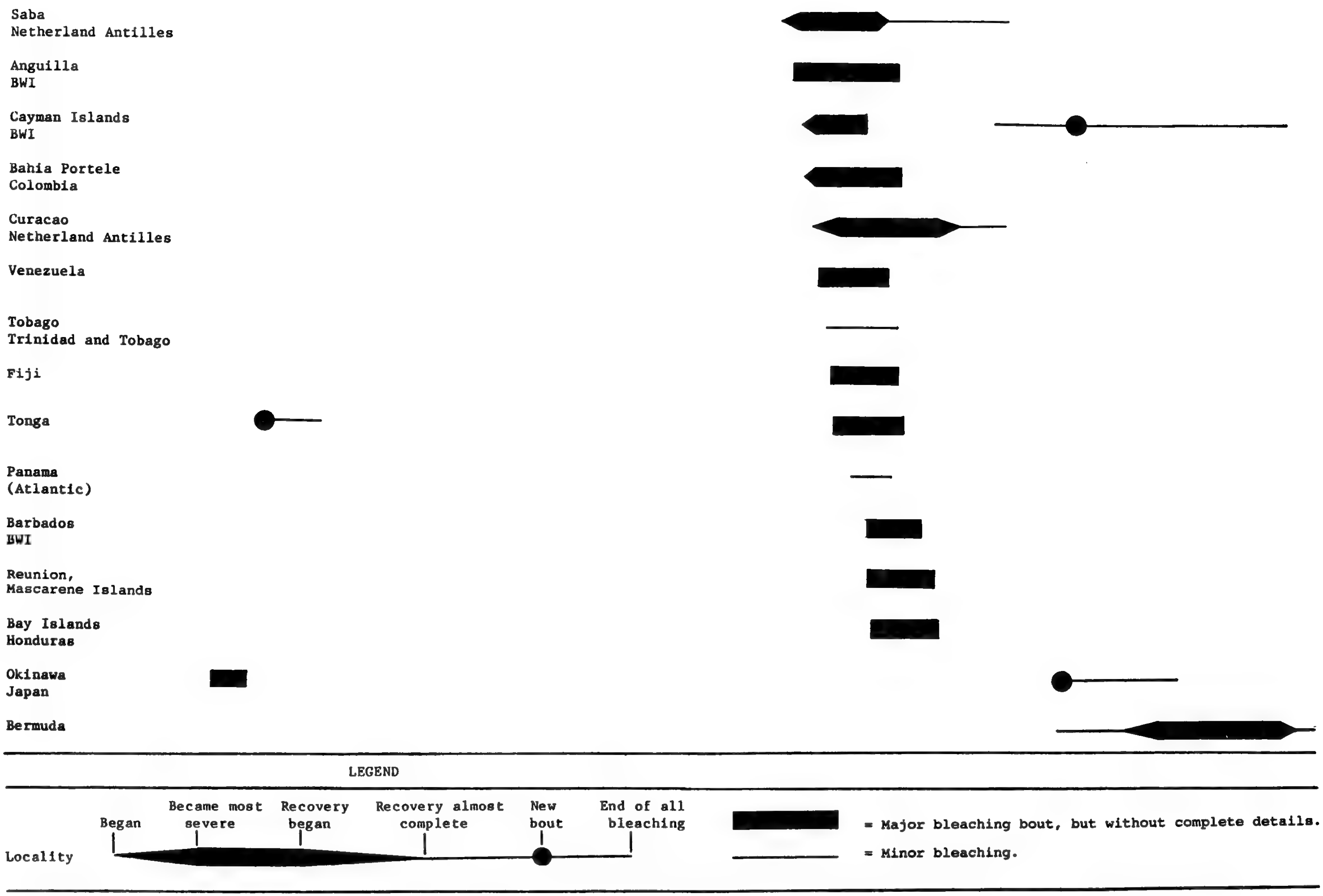


Figure 2: The world from 33°S to 33°N, Part 2: Eastern Atlantic to Western Pacific. 1979-80 Coral (Part 2) Reef Bleaching Sites Marked with Arrows, the 1982-83 with Squares and Rectangles, the 1986-88 in Circles and Elipses.

Figure 3. Progress of the 1986-1988 World-wide Bleaching Events.




Key Largo
Floridas, USA
Gulf of California
Mexico
Puerto Rico
British Virgin
Islands
San Salvador
Bahamas
Mona Island
Puerto Rico
Flower Garden
Banks, Texas
Dominican
Republic
St. John, U.S.
Virgin Islands
Lee Stocking
Island, Bahamas
St. Croix,
U.S. Virgin Islands
Oahu,
Hawaiian Islands
Santa Marta
Colombia
Maui, Hawaiian
Islands
Great Inagua
Bahamas
Bonaire
Moorea,
Society Islands


Saba
Netherland Antilles
Anguilla
BWI
Cayman Islands
BWI
Bahia Portele
Colombia
Curacao
Netherland Antilles
Venezuela
Tobago
Trinidad and Tobago
Fiji
Tonga
Panama
(Atlantic)
Barbados
BWI
Reunion,
Mascarene Islands
Bay Islands
Honduras
Okinawa
Japan
Bermuda
LEGEND
Locality
Began
Became most severe
Recovery began
Recovery almost complete
New bout
End of all bleaching
= Major bleaching bout, but without complete details.
= Minor bleaching.

FOOTNOTE FIGURE 3: Locations with adequate data to indicate progress of bleaching are arranged in chronological order by the time bleaching began in 1987-1988 (major bout). Last name(s) without dates refer to the Personal Communications List. Those followed by "(date)" refer to References: KENYA=McClanahan; AUSTRALIA=Zann, Oliver; MAYOTTE 1986=Thomassin, 1987=Faure; GALÁPAGOS & COCOS ISLANDS=Glynn (1988b); MALDIVES=Wood (1988); BIMINI=Bland; LOOE KEY=Causey; HAWAII 1986=Choquette, 1987=Brock; JAMAICA 1987=Woodley, Goreau, Sandeman, 1988=Gates; FLORIDA 1987=Szmant, Jaap, 1988=Szmant, Vose; ARCH. SAN BERNARDO & ISLAS ROSARIO=Lang, Bohorquez; HAWAIIAN ISLANDS=Choquette; TAIWAN=Dai; TURKS & CAICOS=Lott,Lang, Manstan; CULEBRA 1986=Perkins, Mignucci-G., 1987=Perkins, Tucker; KEY LARGO=Jaap; GULF OF CALIFORNIA=Reyes-B.; PUERTO RICO 1986 & 1988=Perez-T., 1987=Williams, Bunkley-W.; BRITISH VIRGIN ISLANDS=Keil; Underwater Safaris; SAN SALVADOR 1987=Crawford, Tozer, 1988=Gerace, Hardy; MONA ISLAND 1987=Kontos, Nieves, 1989=Williams, Bunkley-W.; TEXAS=Lang; DOMINICAN REPUBLIC=Geraldes; ST. JOHN=Szmant, Boulon; LEE STOCKING ISLAND 1987=Lang, Wicklund, 1988=Muscato; ST. CROIX=Gladfelter, Hillis; OAHU 1986=Choquette, 1987=Brock; SANTA MARTA=Duque, Zea; MAUI 1986=Choquette, 1987=Brock; GREAT INAGNA=Hardy; BONAIRE=Newton; MOOREA=Richmond; SABA=Hof; ANGUILLA=Lang; CAYMAN ISLANDS 1987=Smith, Sefton; 1988=Hayes & Bush (1989); BAHIA PORTELE=Solano; CURAÇAO=-Sybesma; VENEZUELA=Losada (1988); FIJI=Beckman; TOBAGO 1987=Laydoo, 1988=Boyle; TONGA=Bondurant; PANAMA=Knowlton; BARBADOS 1986=Tomascik, 1987=Hor-rocks; REUNION ISLAND=Naim; HONDURAS=Cruz; OKINAWA 1986=Tsuchiya et al.(1987), 1988=Walker, Muzik, Sakai; BERMUDA=Cook, Hagan & Katz (1988), Katz & Hagan (1989)

HOSTS AND NON-PHOTOSYMBIOTIC ANIMALS THAT BLEACHED

Williams and Bunkley-W. (1989) noted approximately 84 species of hosts in 3 phyla and 4 orders from 34 countries and/or islands in the Western North Atlantic. The following additional records (Table 2) add 5 species, 2 orders, and 1 country to their (loc. cit.) list.

Table 2: Photosymbiotic Hosts Bleached in the Western North Atlantic.

SPECIES	LOCATION	DATE	SOURCE
Agaricia sp.	Puerto Rico	1987	Acevedo PC
Agelas conifera[1]	Mona Island, PR	1987	Kontos PC; Ruetzler PC
Colpophyllia sp.	Puerto Rico	1987	Acevedo PC
Diploria sp.	Puerto Rico	1987	Acevedo PC
Eusmilia fastigiata	Tobago	1987	Risk PC
Hymeniacidon(?) sp.[2]	Mona Island, PR	1987	Kontos PC; Ruetzler PC
Iciligorgia schrammi	Mona Island, PR	1987	Kontos PC; Ruetzler PC
Meandrina meandrites	Tobago	1987	Risk PC
Millepora complanata	south Florida	1987	Ferrer PC
	Cuba	1988	Ibarra-M. PC
Montastrea annularis	St. Lucia	1987	Lang PC
	Grand Bahama Island[3]	1987	Waldner PC
Mycetophyllia lamarckiana	Puerto Rico	1987	Goenaga et al., 1989
Oculina varicosa	south Florida	1988	Vose PC
Plakortis sp.[4]	Mona Island, PR	1987	Kontos PC; Ruetzler PC
Porites astreoides	St. Lucia	1987	Lang PC
	Bermuda[5]	1988	Hagan and Katz, 1988
Siderastrea radians	south Florida	1988	Vose PC
Unidentified sponges	Puerto Rico	1987	Acevedo PC
Xestospongia muta[6]	Mona Island, PR	1987	Kontos PC; Ruetzler PC

[1]USNM#41423. [2]USNM#41425. [3]Noted by us in a video by Waldner. [4]USNM#41421-41422. [5]Published photograph. [6]USNM#41424.

Table 3: Photosymbiotic Hosts Bleached in the Indo-Pacific.

SPECIES	LOCATION	DATE	SOURCE
Acropora sp.	Maldives	1987	Wood 1988
Acropora spp.[1]	Andaman Islands	1989[2]	Wood PC
	Okinawa	1988	Muzik PC
	Fiji	1988	Beckman PC
Anemones	Maldives	1987	Wood 1988
Alcyonarians[3]	Reunion Island	1988	Naim PC
Cladiella sp.	Okinawa	1988	Muzik PC
Cnidarians[4]	Great Barrier Reef, Australia	1987	Oliver PC
Diploastrea heliopora	Taiwan	1988[5]	Dai PC
Diploastrea sp.	Maldives	1987	Wood 1988
Favia sp.	Maldives	1987	Wood 1988
Favia spp.	Taiwan	1988[5]	Dai PC
Favites spp.	Taiwan	1988[5]	Dai PC
Favites sp.	Okinawa	1988	Muzik PC
Fire corals[6]	Reunion Island	1988	Naim PC
Fungia sp.	Maldives	1987	Wood 1988
Goniastrea sp.	Maldives	1987	Wood 1988
Leptoseris sp.	Maldives	1987	Wood 1988
Lobophytum sp.	Kenya	1987	McClanahan PC
Millepora platyphylla	Taiwan	1987,1988[7]	Dai PC
Millepora sp.	Maldives	1987	Wood 1988
Palythoa tuberculosa	Okinawa	1988	Muzik PC
Pavona sp.	Maldives	1987	Wood 1988
	Cocos Island and Galápagos Islands	1987	Glynn 1989b
Platygyra sp.	Maldives	1987	Wood 1988
	Okinawa	1988	Muzik PC
Platygyra spp.	Taiwan	1988[5]	Dai PC
Pocillopora elegans	Gulf of California	1987	Reyes-B. 1988
Pocillopora meandrina	Hawaiian Islands	1987	Brock PC, Hau PC
Pocillopora sp.	Maldives	1987	Wood 1988
Pocillopora spp.[8]	Gulf of California	1987	Baynes PC
	Hawaiian Islands	1987	Choquette PC
Porites sp.	Maldives	1987	Wood 1988
	Cocos Island and Galápagos Islands	1987	Glynn 1989b
Seriatopora hystrix	Taiwan	1987,1988[7]	Dai PC
Soft corals	Maldives	1987	Wood 1988
	Kenya	1987	McClanahan PC
Sponge	Gulf of California	1987	Reyes-B. 1988
Stony corals	Kenya	1987	McClanahan PC
	Reunion Island[9]	1988	Naim PC
Stylophora pistillata	Taiwan	1987,1988[7]	Dai PC
Stylophora sp.	Maldives	1987	Wood 1988
Symphyllia sp.	Maldives	1987	Wood 1988
Tridacna gigas	Great Barrier reef, Australia	1987	Goggin PC
Tridacna spp.	Great Barrier reef, Australia	1987	Lucas PC

[1]and other damage caused by bleaching. [2]February. [3]a few.
[4]30 species almost the same as in Oliver (1985). [5]November. [6]Some. [7]July to September.
[8]All species in this genus bleached. 80% of the coral cover was affected. [9]20%.

Gladfelter (PC) felt that not all of the species of reef corals in St. Croix bleached. We could find bleached examples of every reef coral species we could identify during the most intense period of bleaching in Puerto Rico. The bleaching may have been more extensive in Puerto Rico than St. Croix. Most reports that we received concentrated on either the most abundant or most bleached local hosts and made no attempt to determine all species bleaching.

A non-photosymbiotic coral, *Stylaster roseus* and the non-zooxanthellate pigments (orange) in a sponge, *Mycale laevis*, bleached (Williams, L. and Williams, 1988; and Williams and Bunkley-W., 1989). The photosymbiotic microorganisms of *Xestospongia muta* and possibly other sponges which bleached are cyanobacteria, not zooxanthellae (Vicente PC). The pigments in 1 monitored *M. laevis*, which bleached before September 1987 off La Parguera, Puerto Rico, returned to the sponge between March 1988 and March 1989. The comments of unknown reviewers (Proc. 6th Intern. Coral Reef Sympos.) that *S. roseus* could not bleach were considered, but a description of many live colonies gradually turning to white along closely monitored transects (Kontos PC) was difficult to dispute. Subsequent observations by the authors at Mona Island suggest that populations of *S. roseus* have drastically reduced, substantiating Kontos' suggestion that these hydrozoans were severely affected by the bleaching event.

Forty-two species were reported not bleached at various western Atlantic locations (Williams and Bunkley-W., 1989). Most of these were reported bleached at other locations or even at the same general location by other observers. Most species were noted unbleached only in single reports.

Table 4: Hosts Not Bleached in 1987 (Only Atlantic Species with Multiple Reports).

SPECIES	LOCATION	SOURCE
Acropora palmata	Bahamas[1], Colombia[1], Florida Florida Keys,[1] Jamaica,[1] Venezuela	Williams & Bunkley-W. 1989
	Mona Island[2]	Nieves PC
Dendrogyra cylindrus	Jamaica, British Virgin Islands	Williams & Bunkley-W. 1989
	Mona Island	Nieves PC
Pavona clivosa[3]	Gulf of California	Reyes-B. PC
Pavona gigantea[3]	Gulf of California	Reyes-B. PC
Pavona spp.[3]	Kenya[4]	McClanahan PC
Porites californica[3]	Gulf of California	Reyes-B. PC
Porites spp.[3]	Kenya[4]	McClanahan PC
Psammocora stellata[3]	Gulf of California	Reyes-B. PC
Sea anemones	Great Barrier Reef, Australia	Oliver PC, Zann PC
	Gulf of California	Reyes-B. PC
Soft corals	Gulf of California	Reyes-B. PC
Sponges	Great Barrier Reef, Australia	Oliver PC, Zann PC

[1]Reported bleached by others at these locations. [2]*A. palmata* also partially bleached at Mona Island and Puerto Rico during the 1989 bout. [3]Most common stony corals in area.
[4]Although 20% of the total stony coral cover was bleached.

Acropora palmata was reported bleached in 40% of the locations in the Atlantic and was the 6th most reported among 84 species noted by Williams and Bunkley-W. (1989). Jaap (in Hollings 1988) suggested *A. palmata* did not bleach during the 1983 event and was little bleached in 1987. At Grecian Rocks in the Florida Keys, no *A. palmata* bleached (Jaap, 1988). Hudson (1988) found only moderate bleaching in *A. palmata* (uniformly reduced intensity of color) in the Florida Keys in 1987. Jaap (in Hollings, 1988) and Nieves (PC) suggested that *A. palmata* was one of the least affected or most resistant species. Our observations in Puerto Rico would agree. It was often found unaffected and the colonies affected were in what might be considered an interrupted bleaching state with large, white, irregular blotches (Williams, L. and Williams, 1988) on a normal or slightly lighter than normal background. Rarely, these blotches would cover 60-80% of a colony, but usually much less. Some

possessed totally white terminal branches of 10-20% of a colony, but no totally bleached colonies were noted. Lang (PC) also found *A. palmata* much less affected in the Bahamas than the similar *A. cervicornis*. Sandeman (1988b) demonstrated in experiments that *A. palmata* is able to regulate its zooxanthellae more effectively than other corals and can withstand higher levels of light and temperature without bleaching. Despite *A. palmata* being frequently noted not to bleach or to bleach only slightly and *A. cervicornis* noted not bleached only once (Hudson, 1988), bleaching of these 2 species is closely coupled in our reports. They occur bleached together in 13 locations, with each occurring alone only once. Their bleaching seems at least circumstantially related.

Dendrogyra cylindrus was noted bleached only in 3 (Puerto Rico, Culebra Island, and St. Thomas) of 35 Atlantic locations (Williams and Bunkley-W., 1989). Nieves (PC) considered this species resistant to bleaching on Mona Island. In Puerto Rico, we rarely found it bleached, and bleaching was in small discolored to white patches on the sides of colonies. We suspect that the prominent and easily recognizable colonies of this coral would not have been overlooked in so many areas, if it had been bleached.

SMALL SCALE FEATURES

Some western Atlantic corals began bleaching on their edges or top and progressed inward or downward, others began at their bases and moved upwards (Williams and Bunkley-W., 1989). A colony of *Acropora cervicornis* in a public aquarium in St. Thomas bleached from the bottom up to the top overnight (3 May 1988) (Nunn PC). In the Indian Ocean, *Acropora* spp. of the Andaman Islands bleached from their bases toward the tips (Wood PC). This is similar to the action seen in white band disease, but the progress of this disease is usually slower than that seen in bleaching. In the Pacific, *Pocillopora* spp. in Hawaii 1987 (and 1986) (Choquette PC) and *P. elegans* in the Gulf of California in 1987 (Reyes-B. PC) began bleaching at the tips and progressed inward and down to the base. *Tridacna gigas* specimens on the Great Barrier Reef bleached in the central portion of the mantle, but retained color on the extreme outer margin (Goggin PC). Other Caribbean hosts became blotched or striped tan and brown or white and tan, before bleaching white; or gradually became uniformly lighter in color (Hudson, 1988; Williams and Bunkley-W., 1989). Some colonies never progressed beyond the patterns described above, possibly because the bleaching process was arrested. These forms were probably less damaged than their "totally" bleached neighbors. Another possible explanation for the various patterns is that different hosts presumably have different strains of zooxanthellae with different physiological tolerances (Gladfelter, 1988). Also, different strains of zooxanthellae may even occur in different parts of the same colony (Sandeman, 1988b).

Table 5: Bleaching of Some Corals Revealed Delicate Colors Normally Concealed by the Color of the Zooxanthellae.

SPECIES	LOCATION	DATE	COLOR	SOURCE
Acropora spp.	Fiji	1988	Glowing-blue	Beckman PC
Montastrea annularis	Dominican Republic	1987	Lavender-blue	Geraldes PC
Porites astreoides	Colombia	1987	Yellow	Lang PC
	Mona Island, PR	1988	Yellow	This Paper
	St. Thomas, USVI	1989	Bright Blue	This Paper
Porites porites	Colombia	1987	Yellow	Lang PC
Siderastrea radians	Caribbean	1987	Lavender-blue	Williams & Bunkley-W. 1989
Siderastrea siderea[1]	Caribbean	1987	Lavender-blue[2]	Williams & Bunkley-W. 1989
Solenastrea bournoni	Colombia	1987	Lavender-blue	Williams & Bunkley-W. 1989

[1]Williams, L. and Williams (1988, p. 85) illustrated a lavender specimen from Puerto Rico.
[2]Acevedo and Goenaga (1986) did not note this color in Puerto Rican bleached specimens in 1985.

The number of individuals bleached within a species, and the amount of surface area bleached from the reports received were used by Williams and Bunkley-W. (1989) to determine that the most intensely bleached areas in the Atlantic were the northern Caribbean, Bahamas and south Florida. Subsequent reports we received agreed with the original analysis. No obvious large-scale patterns were evident in the Indo-Pacific records noted below (Table 6).

Table 6: Proportion of Colonies Bleached of Indo-Pacific Host Species and Areas Affected.

COLONIES BLEACHED IN A SPECIES	SURFACE AREA BLEACHED	LOCATION	DATE	SOURCE
20-100% (50% of many, 80-100% of some)[1]	20-100% (most 100%)	Australia	1987	Oliver PC
From virtually all to only isolated[1]	20-100% (most 100%)	Australia	1987	Zann PC
80% (soft corals)	100%	Kenya	1987	McClanahan PC
20% (stony corals)	20-100%	Kenya	1987	McClanahan PC
Large-scale bleaching		Moorea	1987	Richardson PC
15% of *Pocillopora elegans*	100%	Gulf of California	1987	Reyes-B. PC
Unidentified sponges	9%	Gulf of California	1987	Reyes-B. PC
80% of *Pocillopora* spp.		Gulf of California	1989	Baynes PC
5-10% of *P. meandrina*	100%	Hawaiian Islands	1987	Brock PC
10% of *P. meandrina*		Hawaiian Islands	1987	Hau PC
80% of *Pocillopora* spp. in some areas		Hawaiian Islands	1987	Choquette PC

[1]Highly variable between sites.

In a world-wide bleaching event in summer-fall 1988, which was much less severe and intense than the earlier 1987 bouts, fewer hosts and less surface areas were affected. Williams and Bunkley-W. (1989) found that the geographic areas in the greater Caribbean with the highest percentage of colony surfaces bleached were also the areas in which bleaching occurred first.

Table 7: Percentage of Total Coral Cover Bleached.

% TOTAL COVER	LOCATION	DATE(S)	SOURCE
80-100	Mangroves of S.W. Puerto Rico	1986, 1988	Perez-T. PC
10-15	Gulf of California	1987	Reyes-B. PC
75-100	Okinawa	1987	Muzik PC
20-100	Kenya	1987	McClanahan PC
5-60[1]	Australia	1987	Zann PC
20-50[1]	Australia	1987	Oliver PC

[1]Highly variable between sites.

Some interesting differences occurred between the supposedly very similar *Millepora alcicornis* and *M. complanata* in the southern Caribbean. In Venezuela, similar numbers of each species bleached (50 and 60% out of 200 and 100 colonies respectively) but most *M. alcicornis* totally bleached, while most *M. complanata* only partially bleached (Losada, 1988). High percentages of *M. alcicornis*, but not *M. complanata* also died in some areas of Colombia (Solano-P. PC).

Table 8: Species Most Often or Severely Bleached or Most "Susceptable" to Bleaching.

SPECIES	LOCATION	DATE	SOURCE
Acropora cervicornis[1]	Bahamas	1987	Lang 1988a,c
Acropora palmata[1]	Florida Keys	1987	Jaap 1988
Agaricia spp.[2]	Caribbean	1987	Williams & Bunkley-W. 1989
Diploria labyrinthiformes[3]	Jamaica	1987	Woodley 1988
Diploria sp.[3]	Mona Island, Puerto Rico	1987	Nieves PC
Faviids[4]	Taiwan	1987	Dai PC
Millepora alcicornis	Bermuda	1988	Cook PC
Millepora platyphylla[5]	Taiwan	1987	Dai PC
Millepora spp.[2,6]	Caribbean	1987	Williams & Bunkley-W. 1989
Montastrea annularis[2]	Caribbean	1987	Williams & Bunkley-W. 1989
Montastrea cavernosa[3,7]	Jamaica	1987	Sandeman 1988b
Palythoa caribbea[2]	Caribbean	1987	Williams & Bunkley-W. 1989
Porites astreoides[3]	Mona Island, Puerto Rico	1987	Nieves PC
	Bonaire	1979	Hof PC
Porites porites[3]	Mona Island, Puerto Rico	1987	Nieves PC
Seriatopora hystrix[5]	Taiwan	1987	Dai PC
Siderastrea siderea[3,7]	Jamaica	1987	Sandeman 1988b
Soft corals	Kenya	1987	McClanahan PC
Stylophora pistillata[5]	Taiwan	1987	Dai PC

[1]Possibly complicated by White Band Disease. [2]These species, representing 3 cnidarian orders, were also similarly listed in most reports received after the Williams and Bunkley-W. (1989) paper. [3]Among others we also listed above (footnote #2). [4]Low temperatures. [5]High temperatures. [6]Although Sandeman (1988) and Woodley (1988) found few *Millipora* spp. bleached in Jamaica. [7]Not listed by Woodley (1988) as most bleached in Jamaica.

LARGE SCALE FEATURES

Williams and Bunkley-W. (1989) simply summarized the maximum depths where bleaching was found in the greater Caribbean as the approximate limits of zooxanthellae. Most of the maximum depth estimates available were subjective observations by SCUBA divers from shallow depths. Later submersible and remote operated vehicle (ROV) observations corroborate deeper records (Table 9). These exact observations cannot rule out bleaching at even greater depths as the most severe bleaching had ended before the submersible and ROV observations were made. The small number of observations below 60 m in Puerto Rico may have missed the fewer colonies bleached at these depths. Smith (PC) found few below 60 m and Lang (PC) found approximately 3% of the colonies bleached at 91.4 m. Indo-Pacific reports did not relate depths of bleaching to the total depth range of hosts present; therefore, it is not clear if bleaching was depth related (Table 9).

Most of our reports and Bohorquez (1988), Jaap (1988) Jaap in Hollings (1988), Knowlton (1988) Lang (1988a,c) and Lang in Hollings (1988) indicate either uniform bleaching in shallow to moderate depths or more intense bleaching in the shallows. Other reports indicate a great variation in local bleaching patterns (Table 10).

Some of the patterns of bleaching around islands (Table 11) may be due to distribution of corals rather than bleaching. Most coral reefs and most SCUBA diving in Barbados occurs along the west coast; therefore, most reports would be expected to originate from this area. However, Vicente (PC) was able to confirm bleaching along the north coast of Puerto Rico, where few corals exist, by the presence of intensely bleached, white *Xestospongia muta*. Muzik (PC) noted that many

Table 9: Depths of Bleaching in 1987.

DEPTH (METERS)	LOCATION	SOURCE
CARIBBEAN		
1-40	Caribbean	Williams et al. 1987
1-60	Caribbean	Williams & Williams 1987
60.0	Southwestern Puerto Rico[1]	Bunkley-W. unpub. data
73.2[2]	Lee Stocking Island, Bahamas	Wicklund in Hollings 1988
85.3	Cayman Islands	Smith PC
91.4	Lee Stocking Island, Bahamas[3]	Lang PC
INDO-PACIFIC		
to 2	Kenya	McClanahan PC
0-6	Great Barrier Reef, Australia	Oliver PC
to 13	Mayotte Islands	Thomassin PC
3-15	Gulf of California	Reyes-B. 1988
to 20	Hawaii	Brock PC
1-21	Hawaii	Hau PC
Shallow to 30	Maldives	Wood 1988
1-40	Great Barrier Reef, Australia	Zann PC
Down to 45	Hawaii	Choquette PC

[1]Remote operated vehicle operations. [2]Based at least partially on bleached sponges and there is some question whether sponges which are normally photo-symbiotic in the shallows possess these photosymbionts below 37m (Vicente PC). [3]Submersible operations.

Table 10: Most Intensely Bleached Habitats or Depth Ranges.

SITUATION	LOCATION	DATE	SOURCE
Intertidal areas	Moorea	1987	Richmond PC
Intertidal areas	Okinawa	1987	Sakai PC
Lagoonal areas	Kenya	1987	McClanahan PC
Lagoon and shallows	Fiji	1988	Beckman PC
Lee sides of reefs	Culebra Island, PR	1987	Perkins PC
Intermediate depths	St. Croix, USVI	1987	Gladfelter PC
Intermediate depths[1]	Jamaica	1987	Smit.-V. PC
Intermediate depths	Grand Turk[2]	1987	Harrigan PC
Intermediate depths	Cuba	1988	Alcolado PC
Intermediate depths	Tobago[3]	1988	Boyle PC
Increasing with depth to 14 m	Culebra Island, PR	1987	Tucker PC
Increasing with depth to 55 m	Bahamas	1987	Lang 1988a,c & Lang in Hollings 1988
Fore-reef slopes	Culebra Island, PR	1987	Tucker PC
Ocean fore-reef[4]	Jamaica	1987	MacFarlane & Goreau 1988
Deeper, drop-off areas[5]	Turks and Caicos	1987	Lott PC
Uniform at all depths	Maldives	1987	Wood 1988

[1]At some sites. [2]Turks and Caicos. [3]Trinidad and Tobago.
[4]Twice as intense as on the protected back reef. [5]Less bleaching in shallows.

areas of the coast in Okinawa cannot bleach because no live corals remain. A rumor has also been received about bleaching along 1 side of Malaysia and not the other. Unfortunately, no details are available to substantiate this pattern (Halas PC, Lang PC).

Table 11: Patterns of Bleaching Around Islands or in Island Chains.

SIDE(S)	LOCATION	DATE	SOURCE
South coasts[1]	Cayman Islands	1987	Williams & Bunkley-W. 1989
South coast[1]	Culebra Island, PR	1987	Williams & Bunkley-W. 1989
South coast	Maui, Hawaiian Islands	1987	Hau PC
Southernmost island[1]	Hawaiian Chain	1987	Brock PC
North coast[1]	San Salvador, Bahamas	1987	Gerace PC
West coast	Barbados	1987	Horrocks PC
West coast	Hawaii, Hawaiian Islands	1987	Hau PC
West coast[1,2]	Maldives	1987	Wood PC
All but east coast	Bonaire	1979-80	Hof PC
All but southeast	Mona Island, PR	1987	Kontos PC

[1]More intensely bleached.
[2]Some, but not all reports supported this pattern on western sides of atolls.

The opposing inshore/offshore patterns of bleaching in Venezuela and Panama at the same time are perplexing (Table 12). The coral reefs along the eastern Pacific were so devastated by the 1983 bleaching and other impacts which followed (Glynn, 1984a,b; 1985a,b; 1988b) that few hosts may be available in many areas to indicate bleaching. However, some reports would be expected and we received none along this coast for 1987-88, except in the Gulf of California. Lang in Hollings (1988) suggested that the early bleaching in Florida and western Caribbean coast of Colombia (Table 12) was due to more "artificial stresses" on continental reefs in comparison with insular areas. Additional data (Fig. 4) suggest that the Caribbean coast of Colombia was possibly not one of the earliest areas to bleach, but it remains the only Atlantic area out of south Florida, Bahamas and the northern

Table 12: Inshore vs. Offshore Bleaching Patterns.

INSHORE	OFFSHORE	LOCATION	DATE	SOURCE
+[1]	–	Australia	1987	Oliver PC, Zann PC
+[2]	–[3]	West Indies	1987	Lang in Hollings 1988
–[4]	+	Florida Keys	1987	Hunt PC
–[2]	+[5]	Central America	1987	Glynn 1988b,1989b
–	+[6]	Barbados	1987	Horrocks PC
+	–	Venezuela	Late 1987	Williams & Bunkley-W. 1989
–	+[7]	Panama (Caribbean)	Late 1987	Williams & Bunkley-W. 1989
–	+[1]	Bermuda	1988	Cook PC

[1]More bleached. [2]Continental coasts, early bleaching. [3]Insular areas. [4]Less bleached.
[5]Galápagos and Coco Islands. [6]Bank reefs. [7]San Blas Islands.

Caribbean which bleached intensely in the 1987 event. The mix of inshore/offshore data suggests the importance of local conditions or local effects in the 1987-88 portion of the event, and the perplexing variability which characterizes this disturbance.

Geographic spreading in this event must remain unconfirmed. It is a process which was unfortunately beyond the scope of the then existing small-scale experimental work (Table 13). Woodley (1988) noted reports of bleaching at Montego Bay to the west of Discovery Bay on the north coast of Jamaica and at Port Royal on the south coast in December 1987. This might indicate spreading, but Smit-V. (PC) noted bleaching at Montego Bay and other areas on the north coast in mid-September 1987. No reports suggested geographic spreading of this event in the Indo-Pacific. The bleaching in 1987 (and 1986) in the Hawaiian Islands seemed to begin on all the islands at approximately the same time (Choquette PC).

Table 13: Geographic Spreading of Bleaching.

MOVEMENT	LOCATION	DATE	SOURCE
South to north	Bahamas	1987	Williams & Bunkley-W. 1989
South to north	Florida Keys to south Florida	1987	Williams & Bunkley-W. 1989
South to north	Looe Key to Dry Tortugas	1987	Jaap 1988
North to south	Looe Key to West Palm Beach	1987	Jaap 1988
West to east	north coast of St. Croix	1987	Williams & Bunkley-W. 1989
West to east	Colombia to Venezuela	1987/88	Williams & Bunkley-W. 1989
North coast to off shore	from St. Croix to Buck Island[1] (north of western end)	1987	Hillis PC

[1]Noted more than a month after the north coast of St. Croix.

Our suggestion that the 1987-88 events were, overall, the most extensive and severe ever reported is based on a combination of parts of many reports. In some cases local observers suggested that the event was the largest ever (Table 14). An unconfirmed report of bleaching was received from the north coast of Australia at Darwin (Zann PC). Bleaching was not documented from other areas of the north coast, but few observations were made during the time of this event in those remote areas.

Table 14: Most Severe and Extensive Bleaching Ever Reported.

LOCATION	DATE	SOURCE
Atlantic	1987-1988	Williams & Bunkley-W. 1989
Great Barrier Reef, Australia	1987[1]	Zann PC
North coast of Australia	1987	Zann PC
Maldives	1987	Wood 1988
Hawaiian Islands	1986, 1987	Choquette PC
Florida reef track	1987	Causey PC, Jaap PC
Bahamas	1987	Wicklund PC

[1]May be the most extensive.

The potential extent of bleaching in the eastern Pacific in 1987 and Okinawa in 1988 will never be known because many of the more sensitive hosts were already dead. This may be true of other areas of the Indo-Pacific, or possibly, bleaching there was either less severe or less completely reported (Fig. 2). Judging from the reports of bleaching, surface areas of reef affected, number and percentage cover of colonies, and tissue loss and mortalities, the north central Caribbean, Bahamas, and south Florida seemed to be the most intensely bleached Atlantic area in 1987-88. All of the Florida reef tract from West Palm Beach through the Dry Tortugas was affected (Causey, 1988; Jaap, 1988). As early as 10 November 1987, Dill in Hollings (1988) noted bleaching all through the Bahamas. Reports we received later from all of the major Bahamian Islands confirmed his statement. Bleaching occurred all around Puerto Rico, Mona Island, Culebra, and Vieques in 1987-88. Most coral reefs in the British Virgin Islands were bleached. Where observations were made in the Dominican Republic, bleaching was intense and extensive (Geraldes PC). Early in the bleaching event, incomplete reports of intense and extensive bleaching were received from Cuba and Haiti. More information is needed from these areas. Bleaching in the remainder of the greater Caribbean area was less intense and less damaging. Bleaching in these areas (with the exception of the Flower Garden Banks off Texas and the western Colombian Caribbean coast) began in late November 1987 and continued to early January 1988. Despite reports (Palca, 1987; Jaap in Hollings, 1988, Weicker in Hollings, 1988, Wicklund in Hollings, 1988) of bleaching in Bermuda in 1987 (questioned by Lang in Hollings, 1988), no bleaching occurred there. The coral reefs of Bermuda were closely monitored in 1987 and 1988, and no bleaching occurred there until mid-1988 (Cook PC).

The concentration of the first bout in a limited portion of the greater Caribbean region (Table 15) indicates some relationship among these sites or the focusing of some phenomenon which caused the bleaching in this area. After November-December 1987, a less intense, but more widespread effect prevailed. Understanding what these original, diverse areas had in common during this period

Table 15: Bouts of 1987-1988 Events and Additional Bouts in 1989 in Greater Caribbean Area with Some Corresponding Bleaching Noted from the Indo-Pacific.

LOCATION SOURCE	DATE	
BOUT 1 - Most Intense Bleaching - Restricted areas		
Northern Caribbean Bahamas South Florida Texas[1] Colombia[1]	July to early November 1987	Williams & Bunkley-W. 1989
BOUT 2 - Less Intensive - Wider Areas		
Remainder of the West Indies including original areas	November 1987 to January 1988	Williams & Bunkley-W. 1989
BOUT 3 - Much Less Intense Bleaching -Few Areas (or little noted?) - cool water period		
Puerto Rico[2]	February-April 1988	Williams & Bunkley-W. 1989
Bahamas (Lee Stocking)[2]		Lang PC
St. Thomas		Nunn PC

BOUT 4 - Moderate to Less Intense Bleaching - Wide Spread Warm Water Period

Bahamas	Summer-Fall 1988	Muscato PC
Bermuda		Cook PC
Cayman Islands		Hayes & Bush 1989
Colombia		Zea PC
Cuba		Alcolodo PC
Florida Keys		Causey PC
South Florida		Szmant PC
Jamaica		Gates PC
Panama (inshore)		Soong PC
Peter Island and Virgin Gorda, British Virgin Islands		Kohler PC
St. Croix, USVI		Gladfelter PC
St. John, USVI		Kohler PC
St. Lucia		Lang PC
St. Thomas, USVI		Nunn PC
Tobago, Trinidad and Tobago		Boyle PC, Risk PC
Puerto Rico		Present paper

Corresponding Bleaching in the Indo-Pacific.

Fiji	Summer-Fall 1988	Beckman PC
Hawaii		Choquette PC
Indonesia		Tomascik PC
Ishigaki Island, Japan		Muzik PC
Okinawa		Muzik PC, Sakai PC, Walker PC

MINOR BOUT Very Extensive but Moderate Bleaching (only noted where corals were very closely monitored) - Cool Water Period

St. Thomas	March-April 1989	McLain PC
Mona Island, Puerto Rico		This paper
Southwestern Puerto Rico		This paper

Corresponding Bleaching in the Pacific

Gulf of California[3]	March 1989	Baynes PC

[1]Less intense bleaching at same time. [2]Areas intensely monitored at this time.
[3]Very intense and extensive bleaching.

of intense bleaching might help explain this bleaching event. This pattern might indicate a physical effect centered first on the northern Caribbean, Bahamas and south Florida, but later expanding to include all of the greater Caribbean and eastern Pacific. But a simple stimulus would not explain why the secondary bout also occurred in some of the previously unbleached hosts in the most severely affected areas, unless the focused and the more diffuse effects were the same phenomenon and the combined long-term exposure finally overcame more resistant hosts. What this focused portion of the event does show is a regional intensification by some as yet undefined effect. Although the most intense bleaching occurred during the normal, warmestwater period of the year and some inshore

temperatures were unusually high, sea surface temperatures of the greater Caribbean region showed nothing unusual (Atwood et al., 1988). The summer-fall 1988 bleachings may be a separate event, even though bleaching continued at reduced levels throughout 1987-88 at many locations. Whether bleaching continued from the original bout or continued from the intermediate bouts was not clear from our reports. Transect studies coordinated by Lang (PC) may be of more use in answering this question.

A minor amount of natural or "background" bleaching occurs on coral reefs (Table 16).

Table 16: Natural or Background Bleaching Occurring at Low Levels.

LOCATION	TIME PERIOD	LEVELS	SOURCE
CARIBBEAN			
Jamaica (2 sites)	Prior to 1987	very low	Williams & Bunkley-W. 1989
Colombia	Prior to 1987	very low	Williams & Bunkley-W. 1989
Puerto Rico	Prior to 1987	anemones[1]	Ballantine PC
St. Croix	Last 10 years	*Palythoa caribbea* frequently	Gladfelter PC
INDO-PACIFIC			
Great Barrier Reef, Australia	Common	corals[1]	Fisk & Done 1985
Iriomoto Island, Japan	1987	anemones[1]	Yokochi PC
Maldives	Last 15 years	very low	Wood 1988
Fiji	Long-term	very low	Beckman PC

[1]Isolated bleached.

We believe the bleaching (Bouts #2-4, Table 15), after recovery began in many areas, was in excess of "background" bleaching and represented new bouts (or events) of the 1987-88 complex. Recent minor bleaching, usually on a seasonal basis, may have significance in the current events and will be considered later.

Knowing when and where bleaching was absent (Table 17) is almost as important in understanding the patterns and causes of the 1987-88 events as knowing when and where it happened. Unfortunately, few observers were willing to send negative reports. The interpretation of this information is also more difficult. Due to the high variability of the event among localities and even habitats, bleaching may have been missed in limited or casual observations. Hosts can sometimes bleach and recover in 4 weeks (Glynn, 1988b; Tomascik PC); therefore, even a thorough photo-transect at monthly intervals could, theoretically, miss a minor bout. For example, bleaching seems to have occurred on the Caribbean coast of Mexico, although most reports for this area were negative (Table 17). Flagg in Hollings (1988) reported bleaching from Cozumel in 1987 but provided no further details. Roberts (1987) also listed Cozumel, but this was apparently taken from Hollings (1988) without citing the source (Roberts PC). The only other positive report we received was of mottled bleaching of *Siderastrea* spp. and other corals at Cozumel and the Yucatan Peninsula in January 1988 (Garrett PC) which seemed to describe hosts which were recovering from bleaching.

Periods when no bleaching occurred in particular geographic areas (Table 18) would also be very interesting to record. Bleaching in Australia is only known from one event in the mid-1970's (Table 18), 1980, 1982, 1983 (Oliver, 1985) and 1987. Since growth apparently ceases during bleaching (Reese et al., 1988), analysis of cores or sections of coral heads might indicate past bleaching events as reduced or unusual growth rings. Unfortunately, many other factors may cause unusual growth rings (Peters PC). However, Carriquiry et al. (1988) suggest both magnitude and chronology of ENSO events can be inferred from coral cores. Such studies might allow a more complete history of these events and a better understanding of the significance of present bleaching.

Table 17: Areas Noted Not Bleached During the 1987-1988 Events.

LOCATION	DATES	SOURCE
Puerto Morales, Mexico	1987 through April 1988	Jordan-D. PC
Quintanaroo and Cozumel areas, Mexico	1987 through May 1988	Liddell PC
Campeche Bank, Mexico	1987-May 1988[1]	Martinez PC
West Caicos, Turks & Caicos	July 1987	Lott PC
Caribbean coast, Panama	Through November 1987	Jaap in Hollings 1988
Panama and Costa Rica[2]	1987	Glynn 1988b
Samoa, Palao, Guam	January to June 1988	Birkland PC
Kenya[3]	1988	McClanahan PC[4]
Ryukyu Islands (except Okinawa)	1988	Muzik PC[5]
(also Ishigaki Island, Japan	1980[6]	Kawaguti et al. 1981)
American Samoa	closely monitored since 1977[7]	Kluge-E. PC

[1]Monthly examinations. [2]Pacific coasts. [3]Although bleached in 1987. [4]Monitored the areas that bleached in 1987 closely. [5]Called scientists and contacts on other islands. [6]When Okinawa and adjacent islands bleached. [7]40 transects examined each year for *Acanthaster planci* damage.

Table 18: Periods With No Bleaching Prior to the 1987-1988 Events.

LOCATION	TIME PERIOD	SOURCE
Indian Ocean	Never previously[1]	Wood 1988
Tortola, BVI	6 years prior	Keil PC
Easter Island[2]	From before 1930 to mid-1980	Cea-E. & DiSalvo 1982
Australia	Before mid-1970's	Bloomfield in Oliver 1985

[1]However, Guillaume et al. (1983), Faure et al. (1983, 1984) and Glynn (1983. 1984) reported bleaching in the western Indian Ocean.
[2]Unfortunately, we do not know if bleaching occurred there in 1982-83 or 1987-88.

MORTALITIES

Deaths of stony corals, gorgonians and sponges were reported from many areas in the most intensely bleached region in the Atlantic in 1987-88 and some deaths of hosts occurred in almost all areas where bleaching was reported (Williams and Bunkley-W., 1989). Numbers of hosts killed in the Atlantic are being compiled from transect data by Lang (1988b) and will not be duplicated here. Tissue loss was reported most commonly in *Montastrea annularis* followed by *Agaricia* spp. in the greater Caribbean region. However, *M. annularis* was rarely and *Agaricia* spp. were frequently completely killed. At Cane Bay, St. Croix, 40% of *Diploria labyrinthiformes* were bleached and many were dead, while only 15% of *D. strigosa* were affected and smaller areas of each colony remained bleached (Gladfelter PC), an interesting difference between these 2 congeneric species.

Early reports of the 1987-88 coral reef bleaching event listed only zooxanthellate hosts as affected (Williams et al., 1987; Williams, L. and Williams, 1987; Williams, E. and Williams, 1988a). Glynn (1988b) suggested that a difference between the 1982-83 and 1987-88 bleaching events was that damage and mortalities in 1987-88 were restricted to photosymbiotic hosts while in 1982-83, damage and mortality included many non-photosymbiotic animals as well. The number of reports of deaths of non-photosymbiotic animals during the 1987-88 event (Table 20) is still very low, and the vast majority of the organisms affected appear to have been coral reef zooxanthellate hosts.

Table 19: Hosts Dead, Partially Dead (marked), or with Tissue Loss (marked "TL") During the 1987-1988 Event.

SPECIES	LOCATION	DATE	SOURCE
Acropora cervicornis[1]	Bahamas	1987	Lang in Hollings 1988
Acropora palmata[1]	Florida Keys (shallow)	1987	Jaap 1988[2]
Acropora spp.[1]	Colombia	1987	Lang 1988a,c
	Fiji	1988	Beckman PC
Agaricia agaricites (50-100%)	Mangrove areas, Puerto Rico	1986, 1988	Perez-T. PC
Agaricia lamarcki	San Salvador, Bahamas (below 25 m)	March 1988	Hardy PC
Agaricia spp. (20%)	San Salvador, Bahamas (below 20 m)	Fall 1987	Hardy PC
(20%)	Great Inagua, Bahamas (below 20 m)	Fall 1987	Hardy PC
	St. Croix	by March 1988	Gladfelter PC
	Turks and Caicos	Dec. 1987 - May 1988	Lott PC
	Lee Stocking Island, Bahamas	Jan.-late March 1988	Muscato PC
	Panama	1987	Lang 1988a,c
Diploria labyrinthiformes	Jamaica	by May 1988	Woodley PC
	St. Croix	by March 1988	Gladfelter PC
D. strigosa (some)	Buck Island, St. Croix	second bout	Hillis PC
Diploria spp. (TL)[3]	St. Croix	by March 1988	Gladfelter PC
(some)	Lee Stocking Island, Bahamas	after Feb. 1988	Muscato PC
Eusmilia fastigiata	Montego Bay, Jamaica	last few years	Smit-V. PC
Millepora complanata	Florida Keys (shallow)	1987	Jaap 1988[2]
Millepora spp.	South Florida	1987	Lang 1988a,c
Montastrea annularis(TL)	Florida Keys	1987	Hudson 1988
(TL)	Puerto Rico	1987	Goenaga et al. 1988
	Jamaica	by May 1988	Woodley PC
(TL)[3]	St. Croix	by March 1988	Gladfelter PC
(some)	Lee Stocking Island, Bahamas	late March 1988	Muscato PC
Montastrea cavernosa	San Salvador, Bahamas (below 25 m)	March 1988	Hardy PC
Porites sp.	Lee Stocking Island, Bahamas	after 1987	Lang PC
Porites spp.	San Salvador, Bahamas (below 25 m)	March 1988	Hardy PC
Porites astreoides	Jamaica	by May 1988	Woodley PC
All corals (20%)	San Salvador, Bahamas (below 25 m)	March 1988	Hardy PC
Anemones, some	Maldives	1987	Wood 1988
Corals (a few)	Buck Island, St. Croix	first bout	Hillis PC
Corals with dead encrusted areas	Turks & Caicos	Spring 1988	Lott PC
Corals (some)	Curaçao	1987	Sybesma 1988
Corals (partial mortalities)	St. Lucia	1988	Lang PC
Corals (partial mortalities)	Florida Keys	Mid-July 1987	Causey PC

Coral mortality	Mona Island, PR (30-40 m)	1987	Nieves PC
Most stony corals[4]	Maldives	1987	Wood 1988
Most shallow corals	Fiji	Jan.-Feb. 1988	Beckman PC
No significant mortalities	Saba, Netherland Antilles	up to July 1988	Hof PC
Minimum mortalities	Gulf of California	1987	Reyes-B. PC
No mortalities	Cocos Island	1987	Glynn 1988b
No mortalities	Galapagos Islands	1987	Glynn 1988b
Soft corals (90%)	Kenya	1987	McClanahan PC
Stony corals (20-30%)	Kenya	1987	McClanahan PC
Stony corals (many)	Okinawa	1988	Muzik PC
Soft corals (many)	Okinawa	1988	Muzik PC
Overall damage to reef light	Okinawa	1988	Sakai PC
Numerous coral deaths	Reunion Island	1987	Faure PC
Few mortalities	Hawaii, Maui, Oahu (Hawaiian Islands)	1986, 1987	Choquette PC
Many parts of corals dead	St. John, U.S.V.I.	mid-July 1988	Rogers PC

[1]Possibly part of white band disease epizootic (?) or decline of *Acropora* spp. in Atlantic.
[2]Jaap in Hollings (1988) found no major mortalities in beginning, but later noted these.
[3]30-50% of colonies. [4]Stony corals that bleached subsequently died.

Glynn, Perez, and Gilchrist (1985) demonstrated that coral symbiotic crabs in bleached or dead corals possessed fewer egg-carrying females, a higher emigration rate, a slight increase in mortality, and a decline in defensive behavior. They suggested that crabs in bleached corals had been deprived of their food. Invertebrates associated with corals in the Gulf of California became reduced in numbers on coral heads bleached in 1987 and abandoned dead corals entirely (Reyes-B. PC).

Glynn (1988b) reported that some species of corals disappeared from the reefs of Panama, and 2 species of hydrocorals may have suffered extirpation in the eastern Pacific region during the 1982-1983 coral reef bleaching. Some alcyonarians shrank to 1/3 of their original size during the bleaching in Okinawa in 1980 (Yamazato, 1981). Many soft-bodied cnidarians probably contracted or retracted and died unnoticed during the 1987-1988 bleaching events. Many of these hosts may have disappeared before the mortalities could be documented (Table 21).

The decline of *Acropora* spp. in the Atlantic (Table 21) occurred before and during the 1987 bleaching event. We did not monitor this decline in Puerto Rico, but in 1984 we participated in a census of damselfish gardens on a portion of Mario Reef, La Parguera, Puerto Rico, and in 1988 this study was repeated. Most of the lawns were in colonies of *A. cervicornis* in 1984, but in 1988 most were in other corals because of the scarcity of colonies of *A. cervicornis*.

Coral heads with dead tops are common on coral reefs in many areas. This damage is usually blamed on low water exposure, although this pattern is also seen on heads found below lowest water levels. Bleaching also seems to affect the top of coral heads more severely in many cases. In some cases only the upper surfaces bleached or these surfaces bleached more severely; or in the case of uniform bleaching, the upper surface often recovered more slowly, leaving a lighter colored cap long after the remainder of the colony regained normal appearance. Often the tops of coral heads die, while the rest of the colony recovers. Besides in Puerto Rico, *Montastrea annularis* with sloughed tissue on upper surfaces was noted in the Florida Keys (Hudson, 1988) and in Haiti (Goenaga and Vicente PC). Possibly, this commonly observed pattern of colony damage is caused by bleaching.

Robinson (1985) noted the loss of many 100-year-old coral colonies in the Galápagos in 1983. Shinn (1989) and Goenaga et al. (1989) have seen similar losses more recently in Florida and Puerto Rico. Death of these large massive corals is a reason for concern, but the changes that caused their demise may be even more important. Wood (1988) suspects reefs in the Maldive Islands have been so damaged, eroded and overgrown, that stony corals may not be able to recolonize. Lapointe (1989) forsees algal reefs replacing coral reefs in the Caribbean as a direct result of increased nutrification.

Table 20: Bleaching, Death, or Abnormal Behavior in Non-zooxanthellate (N) Hosts, and Non-photosymbiotic Animals.

SPECIES	AFFECT	LOCATION	DATE	SOURCE
Bryozoan colonies	Mortalities	Gulf of California	1987	Reyes-B. PC
Chama sp.	Mortalities	Okinawa	1986	Tsuchiya et al. 1987
Coralline Algae	Mortalities	Okinawa	1988	Muzik PC
Echinoderms (inshore)	Unusual behavior[1]	Florida Keys	1987	Jaap 1988
Echinometra mathaei	Mass Mortality[2]	Okinawa	1986	Tsuchiya et al. 1987
Mollusks (inshore)	Unusual behavior[1]	Florida Keys	1987	Jaap 1988
Mollusks	Mortalities	Florida Keys	1987	Causey PC
Polychaetes(inshore)	Unusual behavior[1]	Florida Keys	1987	Jaap 1988
Revitrona caputserpentis	Mortalities	Okinawa	1986	Tsuchiya et al. 1987
Stichopus sp.	Mortalities	Kenya	1987	McClanahan PC
Strombus gigas	Mortalities	Florida Keys	1987	Berg in Jaap 1988
Stylaster roseus	Bleaching	Mona Island, Puerto Rico	1987	Kontos PC
	Mortalities	Mona Island	1989[4]	This paper
Tunicates	Mortalities	Okinawa	1988	Muzik PC
Urchins	Mortalities (hyperthermia)	Okinawa[3]	1987	Tsuchiya et al. 1987
Xestospongia muta(N)	Bleaching	Caribbean	1987	Williams & Bunkley-W. 1989
Other encrusting organisms	Mortalities	Okinawa	1988	Muzik PC
Other shallow-water animals	Mortalities	Florida Keys	1987	Causey PC
Other sponges(N)	Bleaching & mortalities	Caribbean	1987	Williams & Bunkley-W. 1989

[1]And lethargy probably due to hyperthermia. [2]Accompanied by the bleaching and death of hermatypic corals. [3]But no bleaching was noted in 1987 (Sakai PC). [4]Noted.

Table 21: Disappearance or Decline of Coral Reef Hosts.

SPECIES	OCCURRENCE	LOCATION	DATE	SOURCE
Acropora cervicornis	Die-off	Caribbean	1987[1]	This paper
	Die-off	Bahamas	1987	Lang 1988a,c
Acropora palmata	Die-off	Caribbean	1987[1]	This paper
Many anemones	shrank drastically and apparently died	Caribbean	1987	This paper
Many hosts[2]	Disappeared	Florida Keys	1987	Causey PC
Some hosts	Disappeared	Kenya	1987	McClanahan PC
Sponges[3]	Extirpation	Caribbean	1987[1]	Vicente 1989
Ricordia florida[2,4]	Disappeared	Florida Keys	1987	Causey PC

[1]Prior to. [2]Formerly common. [3]Several species. [4]Reported bleached in the Bahamas and Puerto Rico, but not in the Florida Keys or Florida (Williams and Bunkley-W. 1989).

RECOVERY

Jaap (1988) and Jaap in Hollings (1988) suggested that the density of zooxanthellae in a colony can recover from short-duration bleaching in 6-8 weeks. Hoegh-G. and Smith (1988a) found recovery from 50% loss of zooxanthellae, caused by a 4 hour exposure to 32°C, occurred over 23 days. Gladfelter (1988) suggested that short-term-bleached hosts will recover, but those suffering long-term-bleaching will die. Bleaching in 33 sites over 6 years along the Red Sea coast was found to be a short-term phenomenon of the warm, rainy season (Antonius, 1988). Bleached hosts at Guam, a few years ago, recovered in a few weeks (Birkland PC).

Table 22: Rates or Patterns of Recovery.

SPECIES	RECOVERED	LOCATION	DATE	SOURCE
RATE				
Tridacna spp.	24-48 hrs	Bonaire	1987	Lott PC
Eunicia spp.[1]	quickly	Turks and Caicos	1987	Lott PC
Millepora spp.	first	Caribbean	1987	Williams & Bunkley-W. 1989
	quickly	Turks and Caicos[1]	1987	Lott PC
Shallow corals	quickly	Turks and Caicos	1987	Lott PC
Corals	4-6 weeks	Cocos Island	1987	Glynn 1988b
	4-6 weeks	Galápagos	1987	Glynn 1988b
Agaricia spp. (deep)	last	Caribbean	1987-1988	Williams & Bunkley-W. 1989
	slowest	Cayman Islands	1987	Byrnes PC
Deeper corals	little	Florida Keys	May 1988	Causey PC
	last	Caribbean	1987-1988	Williams & Bunkley-W. 1989
	last	Turks and Caicos	1987	Lott PC
AMOUNT OF RECOVERY				
Anemones	some	Maldives	after Dec. 1987	Wood 1988
Hosts	some	Turks and Caicos	Spring 1988	Lott PC
Hosts	1/4 colonies still bleached	Puerto Rico	May 1988	Goenaga et al. 1988
Agaricia agaricites	90%[2]	South Florida	1987	Ferrer PC
Montastrea annularis	90%[2]	South Florida	1987	Ferrer PC
Siderastrea siderea	90%[2]	South Florida	1987	Ferrer PC
Shallow corals	most	St. Croix, USVI	Jan. 1989	Tobias PC
Corals	largely	St. John, USVI	Mid-July 1988	Rogers PC
Hosts	well advanced	Lee Stocking Island, Bahamas	June 1988	Lang PC
Hosts	Steadily	Jamaica	Dec. 1987-May 1988	McFarlane & Goreau 1988
NO RECOVERY, CONTINUED BLEACHING				
Hosts	–[3]	Maldives	Dec. 1987	Wood 1988
Stony corals	–	Maldives	after Dec. 1987	Wood 1988
Stony corals, gorgonians	–[4]	Puerto Rico	March 1988	Morelock PC
Stony corals	–	Little Cayman, Cayman Islands	March 1988	Sefton PC

Agaricia spp.	–	Little Cayman, Cayman Islands	March 1988	Sefton PC
Deep reefs	–	Florida Keys	March 1988	Lang PC
	–	St. John	Mid-March 1988	Hardy PC
	–	Antigua	Mid-March 1988	Hardy PC
	–	Mona Island	Mid-March 1988	Hardy PC
Agaricia lamarcki	–	Jamaica	May 1988	Woodley PC
Hosts	–	San Salvador, Bahamas	May 1988	Gerace PC
BEGINNING OF RECOVERY		Florida Keys	Mid-Nov. 1987	Causey 1988, Jaap 1988
		Gulf of California	late Nov. 1987	Reyes-B. PC
		South Florida	After Nov. 1987	Causey 1988, Jaap 1988
		Western Colombia	Dec. 1987	Bohorquez 1988
		St. Croix[5]	Mid-Dec. 1987	Hillis PC
FULLY RECOVERED SHALLOW REEFS				
		Puerto Rico	Mid-March 1988	Hardy PC
		Antigua	Mid-March 1988	Hardy PC
		Mona Island	Mid-March 1988	Hardy PC
		Florida Keys	March 1988	Lang PC
		Jamaica	May 1988	Woodley PC

[1]Bleached first. [2]100% bleached on 25 Sept. recovered to 10% bleached on 7 Dec. 1987. [3]Widespread bleaching. [4]Photograph taken by Morelock PC. [5]But also new bleaching.

Hudson (1988) noted splotched patterns of coloration in recovering corals in the Florida Keys, and Newton (PC) reported bicolor patterns in recovering corals in Bonaire. The various color patterns and shades of recovering colors were similar to the ones found in the beginning of the bleaching process, and to those of partially bleached corals. Only by following individual corals, can recovery be differentiated from new bleaching or partial bleaching.

Glynn and D'Croz (1989) histologically demonstrated that corals in the eastern Pacific had not completely recovered from bleaching 2 years after the 1983 event. Suharsono (1988) found that the reefs damaged by bleaching in Indonesia in 1983 had not completely recovered in 4 years.

Following the 1987-88 coral reef bleaching events and despite continuing occurrence of disease in many coral species, Bythall (1989) found "encouraging signs of substantial levels of recruitment in many areas" at Buck Island, St. Croix, USVI. This was part of a long-term monitoring program on the reef at Buck Island. Yoshioka and Buchanan (PC) also noted coral recruitment following the 1987-88 bleaching on their long-term study area off southwestern Puerto Rico. We also noted recruitment in areas damaged by the bleaching at Mona Island, southwestern Puerto Rico and St. Thomas, USVI, while at the same time, finding what appear to be increased levels of BBD and continuing WBD.

VARIATION AND COMPARISONS

The description of bleaching in the Caribbean in 1987-88 (Williams and Bunkley-W., 1989) could be best characterized as showing high variation. Few if any trends can be assembled which are not contradicted by some reports. The patterns and extent of bleaching seem to suggest a large number of local, unrelated, practically unique events but they are too highly coordinated to be coincidental. Lang (1987; 1988a,c) and Lang in Hollings (1988) noted high variability among species, locations, habitats, patterns and extent of bleaching in the Bahamas and Colombia, Losada (1988) found similar variation in bleaching in Venezuela, Oliver (PC) in Australia and many of our reports from the Caribbean commented on this variation. Some hosts bleached in only 1 or a few locations in the Caribbean (Williams and Bunkley-W., 1989). Hof (PC) found *Cliona aprica* bleached in Saba,

Netherland Antilles, although Vicente (PC) could not find even partially bleached specimens among the sponges he monitored in Puerto Rico. Losada (1988) found *Briarium asbestinum* commonly bleached in Venezuela, while it was rarely bleached in Puerto Rico, and was only reported to bleach in 3 of 35 locations in the Caribbean (Williams and Bunkley-W., 1989). Sandeman (1988b) found *Montastrea cavernosa* more intensely and more often bleached than *M. annularis* in Jamaica, and Losada (1988) found the same situation in Venezuela. However, most other reports suggested *M. annularis* bleached both more frequently and more intensely than *M. cavernosa*. Woodley (1988) suggested that *M. cavernosa* did not bleach in Jamaica.

Hardy (PC) examined 11 widespread sites in the Bahamas, British Virgin Islands, Saba and Mona Island during the 1987-88 bleaching event. He found San Salvador, Bahamas, to be the most severely bleached area. Bleaching at Key West in 1987 was not as severe as at Looe Key, but in 1983, bleaching had been much worse at Key West than at Looe Key (Jaap, 1988; Jaap in Hollings, 1988). In Colombia, Bohorquez (1988) found bleaching at Islas del Rosario and San Bernardo Archipeligo extensive and similar, but noted less bleaching at Tyrona Park. In the Turks and Caicos, less bleaching occurred on Grand Turk and Providenciales, South Caicos (Lott PC).

In Australia, the 1987 event was similar to the 1982-83 event in timing and species most severely affected (Oliver PC). Bleaching in Florida was more extensive in 1987 than in 1983 or 1973 (Causey, 1988). The 1987-88 events were the most massive known in Florida, exceeding all previous in geographic extent, bathymetry, and longevity (Jaap, 1988). The 1987 event in the western Caribbean coast of Colombia (Lang, 1987; Sanchez-R. and Gomez-R., 1987) was judged in the beginning to be less severe than in 1983 (Lang in Hollings, 1988). Glynn (1988a,b) compared the bleaching in the eastern Pacific in 1983 and the Caribbean in 1987 and found that in 1983 smaller areas were severely affected, branching rather than massive corals were most affected, and non-zooxanthellates were affected. The affected area in the Caribbean was at least twice as large as the areas in the eastern Pacific (Glynn, 1988b), also the area bleached in 1987 in Australia was at least twice the size of areas bleached there in 1982-83, and could be 3-4 times the size if the north coast was involved. Many branching corals were affected in the Caribbean in 1987, and mortalities were higher in branching species in some areas than in massives (although WBD may also be involved). Some non-photosymbiotic animals died during the 1987 event but many more died during the 1983 event in the eastern Pacific. Overall, the 1987-88 event was the most severe, extensive and long-term bleaching ever recorded.

PREVIOUSLY UNREPORTED BLEACHING EVENTS AND COMPARISON TO KNOWN REPORTS

Part of the problem of understanding bleaching events is that the information is patchy and incomplete. In many areas no coral reef scientists are available to make observations. Even when observations were recorded in the past, no "clearing house" for such information was available. Fortunately, in seeking information about the 1987-88 events, some new historic information surfaced. More reports of past bleaching are vital for understanding the patterns and causes of these events.

1969

An intensive and extensive bleaching event occurred on coral reefs of southwestern Puerto Rico in 1969 (Almodovar PC, Atwood PC). The bleaching was probably caused by 38.1 cm of rain during a hurricane that preceded the bleaching (Almodovar PC).

1979-80

In June 1979, an extensive and long-term bleaching event began on Bonaire (Hof PC). It developed progressively and became most extensive and intense in September and October, 1979. The event ended in February 1980. Bleaching occurred on all but the windward coast of the island from 10-40 m depth. Bleaching began in the knobby, columnar form of *Montastrea annularis*. Later it affected other growth forms of *M. annularis* and *M. cavernosa*, *Agaricia lamarcki*, *Colpophyllia natans*, and *Siderastrea* spp. Quantitative transects 90 X 4 m were run 10 September 1979. A transect at 10-15 m depth contained 37 colonies of *M. annularis* bleached, and another at 15-18 m, had 94 colonies bleached. Few if any dead corals were noted during or after the event (Hof PC).

Goenaga and Canals (1979) reported bleaching of *Millepora complanata* in a small area of Puerto Rico in 1979. This damage was apparently caused by lowered salinity and probably was not related to the large scale event in Bonaire.

In the summer of 1980, coral reef bleaching occurred in several areas in the Florida Keys. A massive fish kill which would later spread throughout the Caribbean (Williams, E. and Williams, 1987) was occurring at the same time. The calm, doldrum weather conditions prior to this bleaching event were similar to those preceding the 1973, 1983, and 1987 events in the Florida Keys (Causey PC).

Upton and Peters (1986) found partially bleached, mottled bleached, patchy bleached or bleached specimens with necrosis, of *Agaricia agaricites* in Puerto Rico and Jamaica, *Montastrea cavernosa* and *Meandrina meandtites* in Puerto Rico. Most of these affected specimens were infected with a coccidian that caused the bleaching. Some bleached specimens, however, were not infected. All were collected in the warmest-water period of the year (August-September, 1980) in a year when bleaching occurred in several other widely separated locations.

Bell and Galzin (1988) noted that much of the coral in the lagoon at Mataiva Atoll, died in late 1980, but did not explain why.

1981

Some bleaching of hard corals occurred on the reefs of western and southwestern Puerto Rico in August 1981 (Williams et al., 1987; Vicente PC). A sea surface temperature positive anomaly occurred at this time (temperatures at the shelf break >29°C) and was comparable to a similar one in 1987 (Atwood et al., 1988). Specimens of *Diploria strigosa* and *Porites astreoides* sampled in August 1981 were infected with a coccidian which was capable of causing minor patchy bleaching in other corals (see above) (Upton and Peters, 1986).

1983

Soekarno (PC) found 72 species in 33 genera of scleractinian corals, *Millepora platyphylla*, *M. dichotoma* and some soft corals and sponges bleached on coral reefs of the Seribu Islands (off Jakarta, Indonesia) and the Kaimun Java Islands (off central Java), Java Sea, from March to May 1983. Bleaching began suddenly and affected 40-50% of the corals from the surface to 15 m. The entire surfaces of affected hosts were bleached. Mortalities occurred in 10-15% of the bleached corals with 80-90% of the deaths occurring in mid-May. Not all individuals of each species of host bleached or died in each habitat or depth. Recovery of the surviving hosts began by late July. Bleaching and mortalities were associated with high seawater temperatures. Suharsono in Glynn (1984a) noted, in less detail, what was presumably the same event. Suharsono (1988) has monitored the coral reefs at Pulau Pari, Pulau Seribu (Indonesia) since 1979. In April 1983, seawater temperatures (normal maximum 28°C ±2°C) remained at 33°C for 3 months. Coral cover was drastically reduced by the bleaching.

Bleaching of *Acropora* spp. occurred in the inner shoreline of the southwestern lagoon of New Caledonia in 1983 (Thomassin PC).

1986

Extensive coral reef bleaching of *Pocillopora* spp. began in August 1986 on the Hawaiian islands of Hawaii, Maui, and Oahu from the shoreline to 45.7 m depth. From 20-100% of the surface area of approximately 80% of the colonies were bleached. Bleaching developed progressively over 3-4 months and became most intense in early November. Bleaching seemed to begin about the same time on each island and in all habitats. Water temperatures may have been slightly above normal. Corals recovered with little or no mortality by the end of December. Bleaching started at the tips of colonies and worked its way basally. Selected colonies were tagged and photographed periodically and a 48.3 km section of the coast of Hawaii was examined during the event. Previous bleaching events have not been noted in the Hawaiian Islands (Choquette PC). Three photographs taken during this event by Choquette (PC) seem to be *Pocillopora meandrina*, *P. verrucosa*, *Millepora* sp. and *Porites* sp. In October 1986 on the south coast of the Hawaiian island of Maui, *Pocillopora meandrina*, *P. damicornis*, *Montipora* sp. and *Porites lobata* were bleached from 0.6-10.7 m depth. *P. meandrina* was the most intensly bleached. In November 1986, reports were received of dying

corals in the Napili and Kapalna area. Ninety percent of *Montipora* sp. were bleached, but no *Pocillopora* sp. Reports were also received about bleaching on the island of Hawaii at that time. Calm weather conditions and warm water temperatures occurred during this event (Hau PC).

In May 1986, massive coral reef bleaching and high mortalities occurred on the coral reefs of Mayotte Island (Mozambique Channel) which closely resembled the event there in 1983 (Thomassin PC). The 1983 bleaching event was described by Faure et al. (1983, 1984).

Tsuchiya et al. (1987) found bleaching of coral reef hosts during a mass mortality of urchins in the southern part of Okinawa and on several adjacent small islands in June 1986. Reef hosts in northern Okinawa did not bleach at this time (loc. cit., Sakai PC).

In November 1986, *Agaricia agaricites*, *Stoichactis helianthus* and *Favia fragum* bleached in the mangroves of southwestern Puerto Rico. Approximately half of the colonies of *A. agaricites* bleached over 80-100% of their surfaces. Only 5-10% of the *F. fragum* were affected. Bleaching was slightly more intense in the more shallow and more light-exposed colonies. The onset of bleaching was sudden, and the most intense bleaching occurred in November and December 1986. In some areas half of the *A. agaricites* colonies died. Recovery of the remainder was complete in January of 1987 (Perez-T. PC). This event occurred at the same time of the year as bout #2 in the 1987 events (Table 15).

Also in November 1986, most of the *Millepora* spp., many stony corals and a few gorgonians and sponges bleached in Culebra Island off eastern Puerto Rico. The event seemed to have become intense and widespread suddenly in November, but may have actually started as early as September 1986. *Acropora cervicornis* was the first coral to bleach at depths between 9.1-15.2 m. Later, *Diploria strigosa* and other hosts bleached between 4.6-22.9 m. *Millepora* spp. became totally bleached, most hard corals bleached everywhere except their bases. *Agaricia* spp. bleached along the edges of the colony. Many of the most severely bleached colonies died. Water temperatures may have been a little higher than usual (Perkins PC). Mignucci-G. (PC) also noted bleaching and mortalities of *Acropora palmata* and other corals at Culebra in 1986.

A 2 m high, 3 m diameter colony of *Dendrogyra cylindratus* was completely bleached on the bank reef off Barbados in mid-July 1986. A week later it began to turn brown around the base, 2 weeks later about 25% of the colony had recovered, in 3 weeks the entire colony was a normal color. Some time during the last week of this process, a similar colony 20 m away totally bleached. In 4 weeks the color recovered in the second colony. Twenty neighboring colonies within an approximately 2,500 m radius retained their normal colors. Environmental conditions seemed to be normal during this time (Tomascik PC). This coral was one of the most resistant hosts to bleaching and was never reported totally bleached during the 1987-88 events. Smit-V. (PC) also noted this coral to bleach and recover recently, but prior to the 1987 event, in Jamaica.

Large areas of *Acropora cervicornis* died in the fall (warm water period) of 1986 off San Salvador, Bahamas (Hardy PC). Whether this was due to the 1986 bleaching event or to the WBD epizootic is not known.

UNKNOWN RECENT DATES

Massive bleaching of *Acropora* spp. occurred at Amami Island and Tokuno Island, Amami Islands, Japan, sometime before 1987. It was probably caused by unusually heavy rains coinciding with extremely low (negative) tides as in 1988 in Okinawa (Muzik PC). Bleaching occurred in large patches of corals several years ago in Guam (Birkland PC).

POTENTIAL CAUSES OF THE 1987-88 EVENT

DISEASE

Bacteria (Glynn et al., 1985), a coccidian (Upton and Peters, 1986), fungi (Jaap, 1988, Te Strake et al., 1988), and a ciliate (Nunn PC) have been isolated from bleached corals. The ciliate was only abundant in 1 case and was possibly only associated on necrotic tissue as frequently occurs (Peters, 1984). A perkinsid parasite was found in bleached and/or dying giant clams (Goggin and Lester, 1988; Braley PC, Goggin PC). White band disease (WBD) and black band disease (BBD) were noted in corals bleached in the 1987-88 event. None of these diseases appears to cause major

bleaching events. Physical stresses triggering an infectious disease was suggested as a possible cause of bleaching (Williams et al., 1987). Ruetzler (1988) documented a sponge's photosymbionts (cyanobacteria) becoming pathogens under environmental extremes (such as high water temperatures) and suggested that this is what also happens in BBD. Circumstantial evidence suggests that a parasite in combination with hypothermia killed 36% of the giant clams on some Australian coral reefs (Goggin and Lester, 1988). Onset of bleaching in multiple, widely separated locations was said to preclude the possibility of disease (D'Elia in Roberts, 1987; Jaap, 1988). Many potential pathogens are normally associated with hosts and may not cause disease until hosts are stressed. Spread from a single point of origin, such as in the *Diadema antillarum* mass mortality (Lessios et al., 1984) is an exceptional pattern often found in new diseases (Williams, E. and Williams, 1987). The presence of partially affected and non-affected hosts mixed with bleached ones, might also suggest a pathogen, (Williams et al., 1987) as well as the erratic and multiple bouts of the 1982-83 and 1986-89 events. Failure to transmit a disease condition from bleached grafts to unbleached hosts (Glynn et al., 1985) does not eliminate infectious disease as a possibility. The grafting experiment (loc. cit.) would have exposed a primary pathogen, but the observed bleaching and deaths were more likely caused by a secondary pathogen dependent upon some major degradation of each host's defenses. For the grafts to express a secondary pathogen, a new high temperature bout would be necessary after the grafts were in place. An examination of these grafted colonies after the 1987 event might be instructive.

Williams et al. (1987) suggest that a single disease of the diverse species and phyla of hosts affected was unlikely, but a disease of the more similar photosymbiotic zooxanthellae might be a possibility. However, the addition of hosts with cyanobacteria and non-photosymbiotic animals to the bleaching list (Williams and Bunkley-W., 1989 and present paper) makes the suggestion of a disease of the zooxanthellae less likely.

LIGHT EFFECTS

Fisk and Done (1985) suggested that increased solar radiation with possible unidentified synergistic stresses caused the 1982 bleaching in Australia. Harriott (1985) also suspected radiation as the primary cause, because most bleaching occurred on the upper and unshaded surfaces of colonies in shallow, clear water. However, she (loc. cit.) did note that elevated seawater temperatures occurred, and Oliver (1985) suggested that elevated seawater temperatures were to blame. Light effects were suggested as a possible cause and/or intensifier of the 1987-1988 bleaching (Williams et al., 1987; Williams, L. and Williams, 1987, 1988; Sandeman, 1988a,b; Williams, E. and Williams, 1988a; Woodley, 1988). Evidence for light effects was based largely on bleaching being more pronounced in more exposed areas of effected hosts (loc. cit.). Greater bleaching on upper or more light exposed surfaces of stony corals, gorgonians and zooanthids and/or tissue loss on these surfaces (Hudson, 1988; Goenaga et al., 1988, 1989; Bunkley-W. et al., 1989) was noted in almost all of the reports we received. Gorgonians were sometimes striped white above and below the plane of most direct light (Williams, L. and Williams, 1988). Portions of upper surfaces which fell in shadows of fixed objects were often not bleached (Williams and Lang, 1988). This seems to be one of the few non-contradictory elements in our otherwise highly variable data and seems to indicate a uniform effect of light on bleached hosts. Unfortunately, in some areas, reefs which bleached were obscured by suspended sediments or algae in the water column which precluded light effects during the event. In the Florida Keys, sediment laden waters present in the beginning of the event were replaced later by algal blooms. These effects obscured the reefs from light prior to and during the periods of most intense bleaching (Causey PC). The observed patterns on exposed surfaces there could not have been caused by light. Furthermore, this pattern does not necessarily indicate an increase in light effects. Corals experimentally bleached with increases of temperature, bleached more intensly on light exposed surfaces without any increase in light intensity (Jokiel and Coles, 1977). If the light levels are reduced 10 times, corals can withstand higher temperatures without shedding zooxanthellae (Hoegh-G. PC). This explains the "shading effect". Thus, light and shadow did affect the intensity of bleaching (Goenaga et al., 1988; Jaap, 1988; Jaap in Hollings, 1988; Sandeman, 1988b; and Woodley, 1988) but this is not evidence for increased levels of light as a cause of the bleaching. Microsurfaces of hosts in light are warmer than in the shade (Peters PC). Slight differences may be significant when ambient temperatures are near the levels necessary to cause bleaching.

Woodley (1988) suggested that bleaching of *Montastrea annularis* in Jamaica in depths shallower than 12 m, but not below, was an indication that bleaching was caused by light effects. The

thermocline was at 50 m on these reefs, therefore, temperature caused bleaching should have been uniform to that depth (loc. cit.). Sandeman (1988b) found that no *M. annularis* bleached below 20 m in Jamaica. Assuming that the thermocline and temperature relationships were constant throughout the bleaching event in Jamaica (which has not been established), either synergistic light effects or some depth-related difference in this host caused the observed differences. Sandeman (1988b) suggested that differences in zooxanthellae in different colonies and even different parts of the same colony could explain the different patterns of bleaching. He (PC) found at least 7 different strains of zooxanthellae in *M. annularis* in Jamaica. Battey and Porter (1988) noted *M. annularis* occupies the largest depth distribution of any known photosymbiotic scleractinian coral. The unusual number of strains of zooxanthellae might somehow be related to the unusual depth distribution of this coral. If different strains either occur or predominate at different depths, then these zooxanthellae may allow the hosts to react differently. Other hosts bleached below 12 or 20 m in Jamaica, suggesting that some peculiarity of *M. annularis* was responsible for the observed depth pattern, not a lessening of synergistic light effects with depth. Lott (PC) also found deeper *M. annularis* did not bleach in the Turks and Caicos while *Agaricia* spp. at the same depths bleached.

Jaap in Hollings (1988) suggested that ultraviolet (UV) light does not penetrate well in sea water, and used this as an argument against light effects. He concluded that the bleaching to 70.1 m could not be caused by light. Woodley (1988) used the same assumption as an indicator of light effects. Jokiel (1980) suggested UV light penetrates seawater almost as well as visible light. Coral colonies held in an aquarium in St. Thomas under artificial light also bleached and died during the event (Nunn PC) indicating severe bleaching occurred in the absence of sunlight.

The recent decline in populations of *Chondrilla nucula* in Puerto Rico (Vicente, 1989) may be an indicator of light effects. Exposed sponges have become overgrown by filamentous algae while more protected specimens were not affected (loc. cit.). This sponge bleached during the 1987-88 event (Williams and Bunkley-W., 1989) and its decline could be related to this damage. Just as in the case of bleaching, it could also react negatively to the combination of increased temperatures and sunlight exposure.

The best evidence for light-related damage to bleached hosts is the reduced pigments in zooxanthellae remaining in bleached corals (previously discussed). Goenaga et al. (1988) suggest that exceptionally calm seas coupled with reduced water turbidity was a major factor in the mass expulsion of zooxanthellae in 1987-88. However, Hoegh-G. and Smith (1988a,b) suggest temperature increases, not light increases, cause the expulsion of zooxanthellae and that increased light reduces pigments in existing zooxanthellae. We believe that light effects can damage coral reef hosts when the period of the year with the most direct solar radiation coincides with a long period of abnormally calm, clear weather. Moving corals to a more shallow position on a reef can cause bleaching, presumably because of increased levels of light (Acevedo and Goenaga, 1986; Sandeman, 1988b). Greater water clarity from a gradual reduction of suspended material, and less diffusion at the surface in extremely calm seas, might similarly increase the amount and intensity of light received by corals. Some damage and synergistic effect of light probably occurred during the 1986, 1987-88, and 1989 bleaching, but increased seawater temperatures were most probably the primary cause.

LOW TIDES

Sea level drops associated with El Niño Southern Oscillation (ENSO) events caused mass mortalities of reef-flat animals on Guam (Yamaguchi, 1975) prior to the 1982-83 event, on Moorea Island (south Pacific) and Nukunona Atoll (central Pacific) in 1983 (Glynn, 1984a), in French Polynesia (Salvat in Glynn, 1988) and probably again in Moorea in 1987 (Richmond PC). Low tides were involved in the Florida Keys' 1987 event (Causey, 1988), in bleaching and mortalities in 1988 in Fiji (Beckman PC), in mass mortalities and bleaching in Okinawa in 1986 (Tsuchiya et al., 1987), and extremely low tides 16-17 May 1988 in the Okinawa bleaching (Walker PC). Drastic sea level drops produce bleaching and extensive mortalities, moderate drops may intensify the effects of elevated temperatures and solar radiation.

DOLDRUMS

Unusually calm days with little or no wind or sea movement were noted before and during the event in Puerto Rico, Florida (Causey, 1988; Hudson, 1988; Jaap, 1988; Shinn PC), Mona Island

(Kontos PC), Australia (Oliver PC, Zann PC) and in the Hawaiian Islands (Hau PC) in 1987 (and in 1986 - Choquette PC, Hau PC); and in Jamaica (Gates PC) and Florida (Causey PC) in 1988. Winds in the Bahamas may have been more from the south, southwest and west than usual (Lang in Hollings, 1988). The summer of 1987 was widely reported to be very calm with lower than usual trade winds (Williams and Lang, 1988). Such "doldrum" conditions often precede major marine ecological disturbances in the Florida Keys (Jaap in Hollings, 1988; Bohnsack PC; Causey PC). Tsuchiya et al. (1987) considered clear, calm weather an important factor in the 1986 hyperthermia mass mortalities and bleaching in Okinawa. These conditions favor local increases in temperature in inshore areas, poor circulation, and the formation of hypersaline waters (Williams and Lang, 1988) and would also favor greater water clarity from a gradual reduction of suspended material and less diffraction at the surface allowing greater penetration of light. The calm conditions in the Florida Keys allowed turbid waters from Florida Bay to remain over the reef before the event and an intense algal bloom to remain over the reefs during the event.

HYPERSALINE WATER

Clear, calm days with high air temperatures may have allowed the development of unusually warm, hypersaline water in confined shallow areas in Florida (Jaap, 1988), the Bahamas (Lang et al., 1989) and possibly in the Maldives (Wood, 1988), Culebra Island (Tucker PC) and other limited areas, that intensified the bleaching process. The hypersaline water formed by this process sank and flowed over the shelf and down in parts of the Bahamas to intensify the bleaching of deeper hosts (to 55 m) (Lang et al., 1989), and may have intensified the bleaching around "inlets" and channels in the reef (Hudson, 1988; Jaap, 1988) and depressions and grooves in corals in Florida (Jaap, 1988) and possibly in other areas (Hardy PC). In the Bahamas, such "underflows" are known to flow daily at low tides for up to 5-6 months of the year (Lang et al., 1989). Particularly severe bleaching along both sides of the Wadu Channel in the Maldives (Wood, 1988) may have a similar cause as suggested for the sides of the channels in the Florida Keys.

TURBID WATER

Turbidity may have complicated and intensified the 1987 bleaching in the Bahamas (Bland PC), Culebra Island (Perkins PC), Florida Keys (Causey, 1988), Andaman Islands (Wood PC), and Mayotte Island, Mozambique Channel (Faure PC). From 12 July to 18 September still, murky waters covered the Florida Key reefs (Causey PC). Warm, turbid waters covered the reefs at Isla del Rosario, Colombia, for at least 1 day in July 1987 (Lang in Hollings, 1988). In September 1987, warm, turbid waters covered the reefs in Santa Marta, Colombia (Zea PC). When bleaching was observed in St. Vincent and the Grenadines, the water on the reefs was turbid (Causey PC). From March through April 1987 in the Maldives, a notable increase in phytoplankton occurred (Wood, 1988). Visability during the bleaching in the Gulf of California was about half of the usual distance (Reyes-B. PC). These conditions could, and in many cases were noted to, contribute to the increase of inshore water temperatures.

EL NIÑO SOUTHERN OSCILLATION

In the Florida Keys, where bleaching has been recorded more frequently than anywhere else, bleaching usually coincides with El Niño Southern Oscillation (ENSO) phenomenon (Scientific Committee on Ocean Research, 1983) of the eastern Pacific (Jaap, 1988; Causey PC). This could indicate that bleaching is associated with global atmospheric disturbances (Williams and Lang, 1988). The 2 most extensive world-wide coral reef bleaching complexes coincided with ENSO years (1982-83, 1986-88). Many physical effects associated with the last 2 ENSO events probably caused or increased bleaching on coral reefs. Three were prominent: (1) elevated seawater temperatures; (2) calm seas; and (3) lowered sea levels. Brown (1987) divided the 1982-83 bleaching events into ENSO-related and non-ENSO-related. ENSO disturbances are now considered to have global effects (Rasmusson and Wallace, 1983; Cane, 1986; Glynn, 1988b, 1989a); therefore, the Caribbean and Florida bleaching in 1983 which Brown (1987) listed as due to increased temperatures, may have been ENSO related. The 1982 event in Australia occurred before the 1982-83 ENSO began and most of the 1988 bouts (and 1989 bout) occurred after the 1986-88 ENSO ceased. The 1979-80 bleaching events also did not

occur in years with an ENSO event [moderate or stronger ENSO as defined by Quinn et al. (1987) or by the Scientific Committee on Ocean Research (1983)]. The disturbances associated with ENSO events are very important in causing or intensifying coral reef bleaching, but bleaching is not simply an ENSO effect.

DETERIORATION

The health of the world's oceans and especially coastal areas is, in general, declining (Jeftic et al., 1988). This is further documented by the increasing numbers of major marine ecological disturbances (Table 23). Sinderman (1988) noted that epizootic ulcerative syndromes in marine fishes world-wide is an indicator of the degradation in the coastal marine environment. He considers the world-wide distribution of coral reef deterioration associated with coral reef bleaching and mortalities to be an analogous example of this trend.

Coral reefs are deteriorating in the Pacific (Gomez, 1988) and the Atlantic (Rogers, 1985; Lang in Hollings, 1988) due to sedimentation, industrial or agricultural chemicals and sewage pollution and eutrophication. Of 103 countries with coral reefs, deterioration of reefs as a result of human activities was reported in 93; damage due to natural events (hurricane, cold temperatures, El Niño associated phenomena and coral predators) in 77 (Wells, 1988). Voss (1989) suggested that the world's coral reefs are deteriorating from unknown causes. In the last 5 years coral reef scientists all over the world have reported alarming incidences of coral reef destruction (Maizan, 1988). Best and Boekschoten (1988) found that opportunistic species which could adapt to the dynamic condition on coral reefs, including the influence of man, were beginning to dominate reefs world-wide. Jaap in Hollings (1988) suggested pollution or contamination may have had a synergistic effect in the 1987 bleaching. Rogers (1985) found many Western Atlantic coral reefs had significantly deteriorated in the last 10 years. Carpenter in Hollings (1988) suggested "all Caribbean reefs" were under "stress". Dahl (1985) found most accessible coral reefs in Polynesia were in various stages of decline. Muzik (1985) found severe and possibly irreversible deterioration of the coral reefs of the Ryukyu Archipeligo. Sudara and Nateekarnchanalap (1988) found coral reefs in the Gulf of Thailand and in the Andaman Sea showed degradation. Hutchings and Wu (1987) found extensive deterioration of the coral reefs of Hainan Island, South China Sea, in 1984. Dustan and Halas (1987) found degradation of a Florida coral reef between 1975 and 1982-83 due to physical disturbances in the shallows and sediments and disease deeper. Porter and White (1988) found degradation of reefs in the Florida Keys at least in the shallows, but less degradation deeper, during a 1983-86 study. Jaap (1988) noted that human activities also affect reef development in Florida and that contamination of the reefs was caused by urbanization of the coastal fringe. Ogden (1989) noted a "precipitous decline in environmental health" of the Florida Keys' coral reefs. Trace metals, halogenated hydrocarbons, PCB's, plasticizing agents and coliform bacteria were found in the sediments and organisms from coral reefs in Florida (Skinner and Jaap, 1986; Glynn and Szmant in Jaap, 1988). Acevedo and Goenaga (1986) found that land clearing was causing rapid degeneration of coral reefs in Puerto Rico. Acevedo et al. (1989) found deterioration of reefs near Ponce, Puerto Rico due to sediment impact. Moore in Anonymous (1988) noted deterioration of the coral reefs in Barbados. Naim (PC) noted chronic nutrient enrichment in corals which bleached at Reunion Island in 1988. Deterioration of coral reefs, possibly, has had a synergistic effect on bleaching. These long-term damages may have also reduced the resilience or the level of resistance of coral reef hosts to disturbances such as bleaching events.

Exceptionally intense bleaching in presumably pristine areas such as the Dry Tortugas (Voss, 1989); San Salvador, Bahamas (Gerace PC, Hardy PC) and Mona Island seems to negate the possibility of human effects and deterioration on intensifying bleaching. Possibly deterioration of coral reefs is no longer localized near disturbances caused by humans. Increased nutrient input disrupts the hermatypic coral reef community (Hallock and Schlager, 1986). Wide-spread increase in nutrification that is detrimental to coral reefs has been suggested by Lapointe (1989) and Shinn (1989).

TEMPERATURE

Brief water temperatures 3-4°C above the normal maximum, or extended periods 1-2°C above the maximum, will bleach corals (Jokiel and Coles, 1977). Yamazato (1981) suggested that bleaching in Okinawa in 1980 was caused by elevated seawater temperatures. The 1980 bleaching in Australia

was shorter and less extensive than that in 1982 or 1983, but similar in species affected. Unfortunately, little detailed information was obtained in 1980 (Oliver, 1985), but the bleaching occurred in the warmwater period as did the 1980 bleaching events in other parts of the world, and all may be related. Bleaching in 1983 was closely correlated with sea warming in the tropical eastern Pacific, Okinawa, Java Sea, Florida Keys, and parts of the western Caribbean (Glynn, 1984a,b; 1988a). Carpenter in Hollings (1988) suggests that temperature caused bleaching in the western Caribbean. Increased temperatures seemed to be the most likely cause of bleaching at Reunion Island (Faure PC), Indonesia (Suharsono, 1988), Seribu Islands and Karimuh Java Islands, Java Sea (Soekarno PC) in 1983. Oliver (1985) and Harriott (1985) suggest that high water temperatures were involved in the 1982 bleaching of the Great Barrier Reef, but Fisk and Done (1985) reported normal summer temperatures before and during the 1982 bleaching in Australia. Glynn (1988a) and Glynn and D'Croz (1989) simulated the temperature conditions of the 1982-1983 ENSO event in the eastern Pacific and produced bleaching, death of corals and histological conditions identical to the original observations. Bleaching in the Galápagos Islands in 1987 occurred at the height of a 2-3°C positive sea surface temperature anomaly (Glynn et al., 1989). Most reports suggested higher than normal temperatures occurred during the 1987 bleaching (Williams, L. and Williams, 1987; Williams et al., 1987; Jaap in Hollings, 1988; Williams and Lang, 1988; Williams, E. and Williams, 1988a,b).

Elevated water temperature was suggested as the cause or as a probable cause of the 1987-88 event (D'Elia in Hollings, 1988; Jaap in Hollings, 1988; Lang, 1988c; Sandemann, 1988a,b; Wicklund in Hollings, 1988; Williams and Lang, 1988; Williams, E. and Williams, 1988a,b; Lang et al., 1989); and for local events in the Bahamas (Wicklund in Hollings, 1988), Colombia (Bohorquez, 1988), Florida Keys (Causey, 1988; Hudson, 1988; Jaap, 1988), Jamaica (Gates in Woodley, 1988; Sandeman, 1988b) and Tobago (Risk PC). Newton (PC) suggests *Agaricia lamarcki* is a cooler water coral found on the intermediate to deep portions of coral reefs. It was the most extensively bleached host in Bonaire in 1987. The pattern of bleaching, most severe in the more shallow portion of its depth range (above 35 m), suggests that temperature caused the observed bleaching (loc. cit.). He also noted above average water temperatures for the last quarter of 1987. Sponges, sea grasses, corals and sea urchins, *Diadema antillarum*, all died and/or bleached during a period of exceptionally high water temperatures in the Florida Keys in July and August 1983, and similar events occurred in 1987 (Causey PC, Table 23). Hyperthermia also killed non-zooxanthellate reef animals in the Gulf of California and Kenya during the 1987 bleaching, as previously discussed. These mortalities suggest that unusually high seawater temperatures occurred on some inshore areas during that time.

Hart and Scheibling (1988) suggested that a positive temperature anomaly in June 1960 caused the increase in populations of sea urchins which destroyed kelp beds in the U.S.A. in the 1960's and 1970's. Glynn (1988b) documents a variety of world-wide damage caused by the 1982-83 ENSO event. Although a variety of destructive ENSO effects were involved (as discussed previously), the most important detrimental effects to marine organisms was the seawater warming accompanying this event. Vicente (1989) documents the demise of a group of sponges from much of the Caribbean related to slight increases in seawater temperatures since early in this century. He also suggests that the epizootic ravaging commercial sponges in the Mediterranean since 1986 until the present (Table 23) may also be related to increases in sea surface temperatures in the Mediterranean Sea. The 1986-to-present time frame also coincides precisely with the present world-wide bleaching events. We do not know the timing of the mortalities of *Chondrilla nucula* in Puerto Rico (loc. cit.) and mangrove sponges in Belize (Ruetzler, 1988) in relation to the bleaching events.

Higher than normal water temperatures were also reported from many areas of the Indo-Pacific where bleaching occurred. Wood (1988) suggested that high water temperatures caused the bleaching in the Maldives. Water temperatures from May to July 1987 were estimated to be 2-3°C higher than normal, and the meterological office, Bracknell, England, considers the February-July sea surface temperatures from the vicinity of the Maldives (75°E, 5°N) to be abnormally high (Wood, 1988). Reyes-B. (1988) suggested the high (>30°C) temperatures in the Gulf of California probably caused coral bleaching, but does not dismiss the possibility of a synergistic effect of light. Beckman (PC) noted high temperatures during the January-February 1988 bleaching and mortalities in Fiji. Lucas (PC) noted bleaching of giant clams on the Great Barrier Reef due to high water temperatures. Goggin and Lester (1988) found that warmwater temperature stress of giant clams infected with parasites (*Perkinsus* sp.) can produce mortalities. Other species in this genus of parasite produce mass mortalities of mollusks during the warmwater periods in North America and Europe (Azeredo, 1989; Table 23). High water temperatures in September-October (27.5° C) were also blamed for the

bleaching in the Hawaiian Islands in 1986 (Choquette PC) and 1987 (Choquette PC, Hau PC). Warmwater temperatures were noted during bleaching in Kenya (McClanahan PC).

No bleaching was recorded from Bermuda in 1987 although coral reefs were carefully monitored (Cook PC). In 1988, Bermuda experienced the warmest summer in 30 years (records of the Department of Agriculture, loc. cit.). Bleaching began with the water temperatures exceeding 29°C. As described previously, a bout of bleaching occurred world-wide during the warmwater period of 1988. Warm, very clear waters, occurred during this event in the Florida Keys (Causey PC), warm, very still waters in Jamaica (Gates PC), and warm and turbid waters in Colombia (Zea PC).

High light intensity caused substantial loss of zooxanthellae pigments in corals in long-term growth experiments (Coles and Jokiel, 1978). Hoegh-G. and Smith (1988a,b) suggest increased levels of light bleach hosts by removing pigments, while increased temperatures bleach by removing zooxanthellae. If this is true for the 1987-88 event, then temperature was the primary cause because those hosts examined possessed 10% (Gladfelter, 1988; Glynn, 1988a) or 10-20% (Reese et al., 1988) of the normal levels of zooxanthellae. However, some increased light effects may also be involved, as the remaining cells possessed reduced levels of pigments (Gladfelter, 1988; Glynn, 1988a).

Porter in Woodley (1988) observed bleaching in deep *Agaricia* spp. for a number of years on transects in Jamaica during the period of warmest water temperatures in October. In 1987, these "October" temperatures were attained several months early and remained several months later than usual (Gates in Woodley, 1988; Sandeman, 1988b). Since these temperatures are known to cause bleaching in a few corals over a short period of time, it is not surprising to find long-term maintanence of these levels to cause massive bleaching. Antonius (1988) also found bleaching in the eastern Red Sea for the last 6 years during the warmwater period of the year. Elevated temperature is one of the few reasonably constant trends that we can find in our highly variable reports. The most intense, extensive and destructive bleaching in 1980, 1983 and 1987-88 has either occurred along with unusually elevated seawater temperatures, or, when temperature data were not available, during the normal warmwater season. Even the 1979, 1982 and 1986 events fall into these warmwater periods. If the less severe mid- to late 1988 bleaching is considered a separate event, these disturbances would also fall largely into this period. This is somewhat obscured in Figure 3, because the warmwater seasons are at different times of the year in the southern and northern hemispheres. Fortunately, the times of highest seawater temperatures follow considerably after the times of most intense direct solar radiation to conviently separate the 2 effects. High water temperatures usually persist much longer than the periods of most direct solar radiation. In the rare case (Bermuda 1988) where both temperature and the onset of bleaching were carefully monitored, bleaching exactly coincided with an unusual increase in the seawater temperature (Cook PC). In the unusual case (eastern Pacific 1983) where exact seawater temperatures were available at numerous locations throughout an event, the bleaching was more intense where temperatures were higher (Glynn et al., 1989). Furthermore, a controlled experiment duplicating the conditions recorded in the eastern Pacific in 1983 has demonstrated that the coral reef bleaching, tissue damage, and mortalities can be caused by temperature alone (Glynn and D'Croz, 1989). While world-wide bleaching events are too complex to have a single, simple cause, temperature seems to be the most important, the unifying or triggering cause.

No unusually high temperatures were recorded in Panama (Knowlton, 1988), and the elevations of temperature at Lee Stocking Island, Bahamas (Lang, 1988a,c), parts of Colombia and the Flower Garden Banks, Texas, were slight (Lang PC). Bleaching was also slight in Panama and Texas and moderate in the beginning in Colombia. Atwood et al. (1988) noted increased sea surface temperatures (SST) occurred off Puerto Rico in 1981 similar to those seen in 1987, but bleaching did not occur in 1981. Actually, some bleaching did occur in Puerto Rico in 1981, but has only recently been noted (Williams et al., 1987). MacFarlane and Goreau (1988) suggested past temperature records show significantly higher temperatures have occurred in Jamaica without noticeable bleaching. The difference in effect can probably be explained by the unusual length of time for the 1987 elevations. While normal SST prevailed over much of the region of most intense bleaching (Atwood et al., 1988), abnormally high inshore temperatures occurred (where measured) in many areas. Since offshore SST's are known to have been lower than inshore temperatures in many locations, the use of offshore SST data in general to discredit inshore temperature as a cause for bleaching over the entire region (loc. cit.) was puzzling. Bleaching was highly correlated with elevated SST in the eastern Pacific in 1983 (Glynn, 1988a; Glynn et al., 1989). The overall seawater temperatures alone (represented by SST) may have not caused bleaching in 1987, as it did in the eastern Pacific and

other areas in the 1983 event. In most areas in 1987, temperature increases which caused bleaching were due to weather conditions that allowed inshore heating and not ocean-wide, elevated seawater temperatures.

In 1987 a second bout of bleaching occurred in November-December (Table 15) when temperatures were falling, and a third bout occurred (February-March 1988) in some areas long after temperatures had dropped. The third bout was possibly a result of a sudden lowering of water temperatures in the Bahamas (Lang PC), upwelling of cooler waters in south Florida (Vose PC), and possibly cool temperatures in Puerto Rico. The March-April 1989 bout in the Gulf of California was caused by low water temperatures (Table 15)(Baynes PC), and those at Mona Island, Puerto Rico and the U. S. Virgin Islands were associated with the lowest temperature time of the year following an unusually cool spring. A cold current and possibly upwelling (10-14°C) in Taiwan in November 1988 bleached most faviids between 5 and 20 m along the east side of Nanwan Bay (Dai PC). The possibility that coral reef hosts may be more prone to bleaching by low temperature following a severe high temperature bleaching event is suggested by these cold "echo" bouts. These bouts only produced minor amounts of bleaching and do not detract from the assumption that elevated seawater temperatures accompany the most intensive and wide-spread bleaching of coral reef hosts.

If unusual water temperatures caused the world-wide coral reef bleaching events, then temperatures must have increased prior to 1979-80 when these events first occurred and must have increased again between 1979-80 and 1986-88 to cause even more severe events. Partial to short term, limited bleaching has been recorded in recent years (Smit-V. PC) in deep-water *Agaricia* sp. off Jamaica (Porter in Woodley, 1988), for the last 6 years in coral reef hosts in the Red Sea (Antonius, 1988), for 10 years in *Palythoa caribbea* off St. Croix (Gladfelter PC), and for the last 10-15 years in coral reef hosts off the Maldives (Wood, 1988). Chronic bleaching has occurred in Cuba over the last 10 years (Ibarra-M. PC). Whether these minor bleaching bouts were more severe in 1983, 86, and 87 would be of interest, but they are more important in establishing a pattern of bleaching during the last 6-10 years, mostly during warmwater periods. Vicente (1989) noted the continuing temperature increase in the last 50 years, which has eliminated some sponges from the Caribbean. A major predator (sea star) experienced catastrophic decline in the Gulf of California due to prolonged elevated temperatures (Dungan et al., 1982)(Table 23). Lopez (PC) noted mortalities of herrings (*Harengula* spp.) possibly caused by high temperatures in Puerto Rico in the last few years and Vicente (PC) noted less extensive bleaching in Puerto Rico in the warmwater period of 1981. Wood (1988) noted slightly higher temperatures for the last 10 years in the Indian Ocean (Meterological Office, Bracknell, England). Cook (PC) and Katz and Hagen (1989) found the summer of 1988 was the warmest in Bermuda for 30 years. Sea surface temperatures in Puerto Rico have been on an upward trend for the past few years (Corredor PC). Southern ocean temperatures in 1987 were the warmest for the past 100 years (National Climate Program Annual Report 1987, 1988). Buddemeier and Smith (1988) suspected but could not prove that greenhouse effect rises in global temperature have already begun. The 4 warmest years of the last 100 (since temperatures have been recorded by instruments) were all in the 1980's and 1987 was the warmest (Kerr, 1988). Global temperature has increased approximately 0.5°C since 1880. The warming surge since 1965 is raising the temperature of the earth to levels that rival the warmest temperatures since the last ice age (loc. cit.). The decade of the 1980's was significantly warmer than any previous period on record (National Climate Program Annual Report 1987, 1988). Coral reefs may be the first conspicuous casualty of global warming, and certainly indicate how drastic the effects of the predicted warming may be.

MISCELLANEOUS

A number of other potential factors favoring bleaching were reported, but these varied with almost each location. Greater bleaching was reported in areas of increased sedimentation in Puerto Rico (Morelock PC); and more sediments and suspended matter were noted during the event in the Florida Keys (Hunt PC, Bohnsack PC); Bahamas (Bland PC); Mayotte Reef west Indian Ocean (Faure PC). Murky, silted, freshwater runoff was reported in Colombia (Lang, 1987; Sanchez-R. and Gomez-R., 1987; Duque-T. and Zea PC; Solano PC), Venezuela (Losada, 1988), and in Culebra Island (Perkins PC). Siltation damaged reefs in the Andaman Islands (Indian Ocean) which also suffered bleaching (Wood PC). Cyclone "Clorilda" preceded the event in Mayotte Island (Faure PC) and freak high tides and waves caused siginificant damage to coral reefs in the Maldives (Wood, 1988). Abnormal sea level, sea state, disturbances associated with the 1982-83 ENSO event were

summarized by Glynn (1988b). Long-term sediment stress and contamination of coral reefs by urban areas was noted in Florida (Jaap, 1988); and pesticides in coral tissues in Panama (Glynn, 1984a; Glynn et al., 1984). All Caribbean reefs are affected by pollution (Wicklund in Hollings, 1988). Some reefs in Puerto Rico adjacent to urban areas may have bleached more intensly than more isolated areas. A combination of stresses may have been necessary to start the bleaching in some areas (Lang, 1988a,c) and reefs subjected to sediment or pollution seemed to have bleached more intensely (Williams and Lang, 1988). Multiple factors may act synergistically and produce greater bleaching than individual stresses would alone (Coles and Jokiel, 1978; Steen and Muscatine, 1987). Natural coral reef bleaching is usually caused by synergistic effect among several factors (Lang in Hollings, 1988).

COMPOUNDING DISTURBANCES

A large number of major marine ecological disturbances have occurred in the last few years (Table 23). Some of these have had a direct impact on the damage caused by coral reef bleaching and/or the recovery of bleached hosts:

(1) BLACK LONGSPINED SEA URCHIN MASS MORTALITY: Many algae grow more rapidly than corals and would overgrow and smother coral reefs if not controlled by herbivorous urchins and fishes (Little and Littler, 1985). The 1983-84 *Diadema antillarum* mass mortality effectively eliminated one of the potentially most important controllers of algae on western Atlantic coral reefs. This is especially serious where overfishing has already removed many herbivorous fishes (Hay and Taylor, 1985). Rogers (1985) found all shallow water coral reef fisheries in the Western Atlantic had declined due to overfishing and habitat destruction. Lang in Hollings (1988) suggests that almost all commercial fisheries in the tropical western Atlantic are overfished and are highly vulnerable to disruption. Unchecked algal growth is occurring at the expense of reef corals in many central Caribbean areas where this double loss of algae controlling herbivores has occurred (Lang in Hollings, 1988). Carpenter in Hollings (1988) suggested that the great increase in algae on Caribbean coral reefs which in some cases has overgrown and killed corals was an effect of the *D. antillarum* loss. After the *D. antillarum* mortality, algal blooms occurred on many reefs in the Caribbean, recruitment rates of corals became reduced and a reduction of coral cover followed. Some adult corals, gorgonians, zooanthids and sponges were overgrown and killed by algae (as summarized by Lessios, 1988). Acevedo and Morelock (1988), monitoring sediment stressed corals off Puerto Rico, noted colonization by filamentous algae. Many of our reports of the coral reef bleaching in the Caribbean noted rapid growth of algae on bleached and dying corals. Vicente (1989) reports the recent decline of populations of a sponge (*Chondrilla nucula*) due to overgrowth by filamentous algae. Causey (PC) noted large amounts of blue-green algae covering sand areas between corals in the Florida Keys which did not occur prior to the *D. antillarum* loss and Zann (PC) noted large-scale benthic algal blooms on the Great Barrier Reef prior to and during the 1987 event. In the Indo-Pacific, with no diadematid loss (except in the Hawaiian Islands) fewer cases of algal damage have been noted. Cuet et al. (1988) found fleshy algae overwhelming corals on Reunion Island, Indian Ocean. Algal growth was damaging corals in some areas there prior to the 1987-88 coral reef bleaching (loc. cit.). Algae were more abundant on Atlantic reefs after the *D. antillarum* mortality, and may have been more available to take advantage of injured or dying corals, and may have contributed to the damage and mortalities which occurred during the event. Bare skeletal surfaces on colonies were quickly overgrown by algae. The former high abundance of *D. antillarum* might have kept some of the surfaces clear of algae and available for eventual recovery by the colony. All dead areas of colonies (which were followed by those making reports) were quickly overgrown by algae. Another urchin, *Tripneustes ventricosus*, has been drastically reduced in numbers, presumably by overfishing, in Barbados during the 1980's (Scheibling and Mladenov, 1987). Overfishing for herbivorous fishes and urchins will certainly intensify the algae problem on the reefs. Goenaga et al. (1989) noted that *Montastrea annularis* colonies quickly recovered from physical damage prior to the 1987 bleaching, but most areas damaged during and after this event permanently lost tissue.

(2) WHITE BAND DISEASE EPIZOOTICS: In the late 1970's large stands of *Acropora palmata* began to die of WBD. This mortality continued until the majority of this coral in the region was destroyed (Carpenter in Hollings, 1988); loss of *A. cervicornis* has also been considerable. In the

summer of 1980, epizootics of WBD occurred in Curaçao (*Acropora* spp. 70-90% affected) and Jamaica (Rogers, 1985) Between 1981 and 1986 *A. cervicornis* declined 96% at Key Largo, Florida Keys (Jaap et al., 1988). Most colonies of *A. cervicornis*, which was formerly a dominant coral on the reef slopes at about 5 m, Islas del Rosario, Colombia, died during the early 1980's (Lang, 1988a,c). *Acropora* spp. died in Costa Rica and possibly Colombia after the 1983 bleaching event (loc. cit.). *Acropora cervicornis* was reduced 99% a few years ago in Curacao by WBD. Storm damage has hindered the slow recovery of this coral, and recovery may not be complete for another 20 years (van Duyl, 1989). Large areas of *A. cervicornis* died in San Salvador, Bahamas, in the fall of 1986 (at approximately the time bleaching was occurring elsewhere). A mass mortality of *A. cervicornis* occurred off Panama (Knowlton et al., 1988). Mortalities of *A. cervicornis* in the beginning of the 1987-88 event in Jamaica (Woodley PC) and the Florida Keys (Jaap in Hollings, 1988) may have been related to WBD. Mortalities of *A. cervicornis* in the Bahamas (Lang in Hollings, 1988) and *A. palmata* in the Florida Keys (Lang PC) may have been compounded by WBD. Bohorquez (1988) found WBD in some of the corals bleached in Colombia. Some of the bleaching of *Acropora* spp. in the Andaman Islands, Indian Ocean, in February 1987 may have been caused or compounded by WBD. Both WBD and BBD have been noted on these reefs (Wood PC). The combination of WBD and bleaching must be more lethal than either disturbance alone. Fortunately the ongoing study of WBD under the support of Sea Grant (Hernandez-A. PC) and the monitoring of this disease by the Virgin Islands Resource Management Cooperative (Davis et al., 1986) in the U. S. Virgin Islands should provide more information about this combination.

(3) BLACK BAND DISEASE OUTBREAKS: An outbreak of BBD occurred in the Florida Keys from August through September 1987 during the coral reef bleaching event (Causey PC). Dill in Hollings (1988) noted BBD in bleached corals during the event in the Bahamas, and suggested that the disease was expanding in the area. Lott (PC) found BBD only in bleached *Siderastrea* spp. during the event in the Turks and Caicos; Bohorquez (1988) found some BBD in bleached corals in Colombia and Wood (PC) noted BBD from reefs in the Andaman Islands (Indian Ocean) where bleaching damage occurred. BBD occurred in *Diplora clivosa* on Mona island in March 1989. All colonies (300+) of *Siderastrea siderea* and *S. radians* we examined from 4 locations on Mona Island 9-10 March 1989 were either partially bleached and/or diseased, but only a few showed positive signs of BBD. We also noted BBD at 2 sites off southwestern Puerto Rico in *Montastrea annularis* and possibly *S. siderea*. This disease had not been noted at Mona Island or Puerto Rico in previous extensive studies (Goenaga PC). Colonies infected with BBD may be less resistent to bleaching. The outbreaks of BBD in Florida and possibly Mona Island and its spread in the Bahamas during the 1987-88 bleaching event indicate some advantage for this disease in corals damaged by bleaching, possibly a breakdown of resistance. Shinn (1989) found that many corals weakened by bleaching in 1987 subsequently died of diseases.

(4) OTHER DISEASES OF HOSTS: Besides WBD and BBD, a number of other disease conditions have been reported from bleached hosts or from hosts during the time of bleaching. Some of these appear, with the limited information available, to describe degenerative conditions, caused or intensified by bleaching, or possibly by the conditions which caused bleaching. Shinn (1989) suggested that coral diseases were related to the world-wide rise in sea level and an overabundance of nutrients. Gladfelter (1988) suggested that bleached corals may be susceptable to other stresses and D'Elia in Hollings (1988) suggests that they are more susceptable to diseases which can kill corals. A normal skelatal fungus of *Millepora complanata* invaded and decomposed the tissues of this coral during bleaching in 1983 (Jaap in Hollings, 1988; Te Strake et al., 1988) and in 1987 (Jaap, 1988). Vicente (1989) recently found *Chondrilla nucula* succumbing to overgrowth by filamentous algae in Puerto Rico. This sponge also bleached in Puerto Rico during the 1987-88 event (Williams and Bunkley-W., 1989). Ruetzler (1988) describes mortalities of a mangrove sponge caused by its symbiotic cyanobacteria. Unexplained sponge mortalities occurred in Puerto Rico (Williams and Bunkley-W., 1989) and in the Florida Keys (Causey PC) in 1987.

(5) CROWN OF THORNS OUTBREAKS: *Acanthaster planci* damage has probably compounded the coral reef bleaching event by outbreaks which preceeded the 1987-88 disturbance in many areas, and by preying on survivors in others. A new series of *A. planci* infestations began in many areas of the Great Barrier Reef of Australia (and possibly elsewhere in the Pacific) in the late 1970's and

is continuing (Phillips, 1987). Outbreaks of *A. planci* have occurred in the past at intervals of several decades (2-3 times a century), but they are much more frequent now and are chronic in some areas (Birkeland, 1989; Yamaguchi, 1986). Infestations in 1981-83 also preceeded the 1983 bleaching in Mayotte Island (Thomassin PC) and occurred along with bleaching damage in the Andaman Islands (Indian Ocean) (Wood PC). Muzik (1985) found coral reefs of the Ryukyu Archipeligo, Japan, had not recovered from *A. palanci* damage 10 years previously and were largely dead. She (PC) suggests that bleaching was not noted in many areas because too few hosts remain alive to register bleaching. *A. planci* damage to coral reefs may have weakened or predisposed corals to bleaching. Bleaching also increased the vulnerability of some surviving corals, formerly protected by barriers of *A. planci*-resistant corals, when these corals perished in the bleaching event in Panama in 1983 (Glynn, 1985b) and the Maldives in 1987 (Wood, 1988). Corals died during or after the bleaching in many areas, but few reports noted non-photosymbiotic animal damage in 1987-88. Presumably, the ratio of *A. planci* to prey corals may have increased in many areas as a result of the bleaching. Even when non-photosymbiotic animals were damaged, as in the eastern Pacific during the 1982-83 bleaching event, the relative effect of *A. planci* predation intensified (Glynn, 1985b).

(6) OTHER CORALLIVORE/BIOERODER OUTBREAKS: McClanahan and Muthiga (1988) found overfishing on Kenyan coral reefs greatly increased the numbers of the sea urchin, *Echinometra mathaei*, and decreased coral cover. Intense bleaching and host mass mortalities occurred on Kenyan coral reefs in 1987 (McClanahan PC). Whether more intense bleaching occurred on the reefs most damaged by overfishing and urchins was not determined. Sea urchins on some eastern Pacific reefs from early 1983 to at least late 1987 were destroying the reef framework (Glynn, 1988b). Corallivorous gastropods, *Drupella* spp., are causing extensive damage to corals in Miyake-jima, Japan, the Philipines, and Ningaloo Marine Park (western Australia), and dense aggregations occur in much smaller areas at Guam and Enewetak (Birkeland and Eldridge, 1988). Both *Drupella* spp. and *Echinometra mathaei* are extraordinarily abundant around Okinawa (loc. cit.). Of these areas, we have reports of bleaching in 1987-88 only from Okinawa. Knowlton et al. (1988) noted predators at near-normal levels prevented recovery of *Acropora cervicornis* following storm damage in Jamaica and following a mass mortality of this host in Panama. Glynn (1985a,b) and Guzman and Robertson (1988) noted damage by predators to bleaching corals in 1982-83, although the abundance of these predators was no higher than before the bleaching event. A combination of predator/bioeroder outbreaks and bleaching could be extremely serious. Glynn (1988b) found damselfishes established territories in algal patches in necrotic areas caused by bleaching and caused further coral mortalities. We observed a tagged, bleached colony during the 1987 event with a small damselfish garden on its side. This stony coral colony became almost totally engulfed by the garden and died.

(7) RED TIDES: Red tide or dinoflagellate blooms commonly produce mass mortalities of marine animals following El Niño events, but none was reported after the 1982-83 event (Glynn, 1988b) and we only received one report for the 1987-88 event. From March-April of 1987 a toxic dinoflagellate bloom possibly occurred in the Maldives. Reports of "red water" were received from several locations and red scum washed ashore at Lakantinolla. Dead fish (mostly moray eels, trumpetfish, and anemonefishes) were found and many reef fishes were observed to behave in a disoriented manner at this time. Anemones on the reef closed (Wood, 1988). Unfortunately, samples of the apparent dinoflagellate bloom were not preserved. Red tides may have compounded the 1987-88 bleaching event in the Maldives. Red tides have been increasing in frequency of occurrence in the western Pacific since 1975 (Birkeland, 1989; Maclean, 1984).

CONCLUSIONS

WORLD-WIDE BLEACHING EVENTS

The 1987-88 bleaching was the most extensive and widespread ever recorded. It undoubtedly represents a world-wide interrelated disturbance (Fig. 2) as all cases can be arranged in an overlapping time-related representation (Fig. 3). The 1982-83 bleaching events (Glynn, 1984a,b) were less obviously related (Glynn, 1984b, 1988b). The most confusing part of the 1982-83 pattern was the extensive bleaching on the Great Barrier Reef of Australia in 1982, 1 year before the 1983 reports of bleaching. If the 1982 Australian event is temporarily ignored in our analysis, then the remaining disturbances (loc. cit.) seem to represent an interrelated world-wide event. Bleaching also occurred on the Great Barrier Reef in 1983, although it was not as intensive, it was almost as widespread as the 1982 event there (Oliver, 1985).

At least 3 widely separated areas in the Pacific suffered extensive coral reef bleaching in 1980: Australia (Oliver, 1985), Easter Island (Cea-E. and DiSalvo, 1982), and Okinawa (Yamazato, 1981). Mass zooxanthellae loss caused by high seawater temperatures also occurred at Enewetak in August 1979 (Fankboner and Reid, 1981). They (loc. cit.) assumed, without much information, that the expulsion was a routine summertime occurrence and not part of a bleaching event. These incidences were studied and reported separately and no effort was made to discover bleaching in other areas at that time. Bleaching also occurred in Florida in 1980, and a year earlier, extensive bleaching occurred in Bonaire. The wide distribution of the known 1979-80 bleaching sites (see arrows Fig. 2) almost covers as much of the world as the 1983 and 1987-88 bleaching sites, they only differ in the total number of sites. We suspect the 1979-80 events represent a first, possibly less intense and extensive (and/or possibly less well studied), world-wide interrelated bleaching disturbance. What has been recorded may represent only a fraction of the actual bleaching areas in 1979-80. No one expected or tried to confirm world-wide bleaching in 1980. The great distances between the locations of reported bleaching in 1979-80 also suggests that unreported events could have occurred in these areas. After 9 years, enough additional reports to confirm the world-wide nature of the disturbances in 1979-80 may never be obtained.

How else can the events in 1980 be compared with those of 1983 and 1987? Three years separate the first (1980) and second (1983) major events and 4 years occur between the second and third (1987). Each major bleaching event increased in extent and intensity. All 3 disturbances share another similarity, all were preceded by 1 year by extensive bleaching events at 1 or more locations. The 1979 bleaching in Bonaire preceded the 1980 bleaching disturbances by 1 year, the 1982 bleaching in Australia preceeded the 1983 bleachings by a year, and the bleaching at many sites in 1986 preceded the 1987-88 event by 1 year. This brings the 1982 bleaching in Australia, which we deferred comment on before, back into consideration, and explains how it fits into the pattern of world-wide bleaching. Even these "preceding bleaching events" intensified and enlarged. Therefore, the bleaching that occurred in 1979-80, 1982-83, and 1986-88 each formed a bleaching complex that included a preceding event followed by a main event.

CAUSE OF THE 1986-88 EVENTS

The conflicting and contradictory causes reported and suggested among and even within sites makes analysis of the 1986-88 bleaching complex very difficult. The overall elevated temperatures for the 1980's made temperature effects an appealing suggestion for the cause of bleaching. The historic information, both published and new, related all extensive and severe bleaching, and even most minor bleaching, to the times of the year with the highest seawater temperatures, or other times with abnormal temperatures as high as these warmwater periods. The SST data (Atwood et al., 1988) conflicted with a direct temperature explanation, but inshore temperatures at the same time were high enough to cause bleaching, suggesting that poor circulation associated with world-wide ENSO effects was resulting in temperature increases of already very warm inshore waters to levels above that required for bleaching. These 2 ENSO warming effects (direct ENSO warming; and indirect warming inshore due to meterological effects associated with ENSO) explain the most intense and wide-spread of the 1986-88 bleaching bouts, and even explain most of the less intense bouts. Other

ENSO effects which caused bleaching directly, were important at only a few of the reported sites. Other ENSO effects, degradation effects, and light effects may have synergistically intensified bleaching.

CAUSE OF THE 1982-83 EVENTS

Some of the 1982-83 bleaching bouts were probably caused by obvious increases in overall seawater temperature as indicated by the SST data (Glynn, 1984a; Glynn et al., 1989). Much of the remainder was probably due to ENSO effects which allowed local, inshore temperature to increase as in 1986-88. Since many local temperatures were not recorded or recorded for only brief periods, the role of temperature cannot be determined for many areas. The 20 temperature recorders in place in the Caribbean in 1988 (Wicklund PC) may help to obtain this information for future events just as a recorder in place on the coral reef in Okinawa confirmed temperature as the cause of the 1980 coral reef bleaching there (Yamazato, 1981). The underlying cause was again probably the increase in temperatures world-wide and the deterioration of coastal areas and coral reefs all over the world.

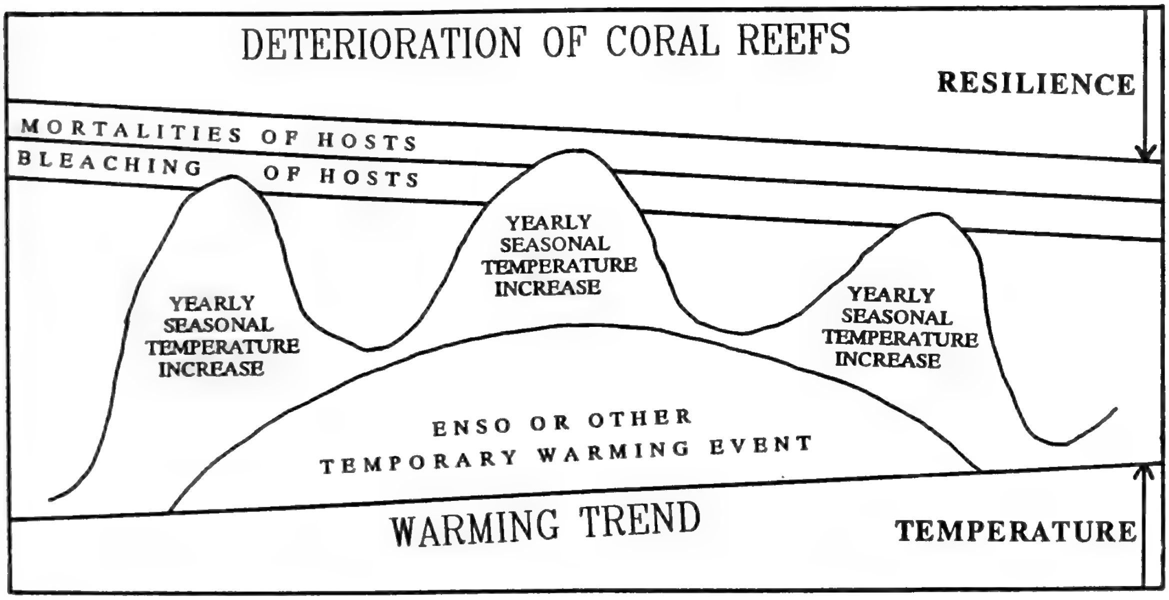


Figure 4: Model of the causes of world-wide coral reef bleaching. Elevated temperatures sufficient to bleach hosts are attained seasonally when augmented by the general warming trend and ENSO or other temporary warming events. The general deterioration of the coral reefs has lowered the resilience of the hosts making bleaching damage more serious. The three seasonal peaks of temperature also represent the preceding, main, and following events as shown in Figure 1. The preceding and following events only cause bleaching because they are on the "shoulders" of the temporary warming event; while the main event produces more severe bleaching and mortalities because it occurs at the height of the temporary warming event.

THE 1991 OR 1992 CORAL REEF BLEACHING EVENTS

Our analysis of bleaching in the last decade, shows that three bleaching complexes have occurred suggesting a cyclic phenomenon (Fig. 1), probably riding on a progressively higher base of elevated temperature and increasing reef deterioration. If our model (Fig. 4) is correct, bleaching cycles will continue to occur on average every 3 to 4 years, with another bleaching complex predicted to begin with a preceding event in 1990 or 1991 and becoming a major world-wide bleaching event in 1991 or 1992. By our model, we expect the event to be more severe and more extensive than the others.

Since bleaching complexes also depend on the next moderate or strong ENSO event and these occurrences cannot be predicted (Glynn, 1988b), the start of the next bleaching complex cannot be exactly pinpointed.

PRECEDING AND FOLLOWING EVENTS

The 1979-80, 1982-83, and 1986-88 coral reef bleaching complexes were divided into "preceding" and "main" events; in addition, in the 1986-88 complex a "following" event was also observed. Each of these events center around the warmwater period of each year. Even during an ENSO warming event, temperatures in most areas are highest during the normal warmweather periods. A general background warming over 2 years (1979-80 or 1982-83) includes 2 warmwater periods; over 3 years (1986-88), 3 warmwater periods. The reason preceding and following events are less intense and less destructive than main events is that they occur in the beginning or ending of the warming trend, when warming is less intense; while the main events occur at the height of the background warming effect (Fig. 4).

Part of the problem in studying major marine ecological disturbances (MMEDs) is the lack of warning and the speed of these events. This makes research efforts difficult to plan and standard research funding almost impossible to obtain on such short notice. In 1979, a potential year-in-advance warning of major coral reef bleaching (1980) first occurred. In 1982, this same warning was repeated but no one was recording, much less analyzing, these events. This warning devise should have been recognized and used at least by 1986 when it was repeated for the third time. The coral reef scientific community should have had a year (1986-87) to prepare for the study of the most extensive world-wide bleaching event ever recorded (1987-88). How much knowledge have we lost because of failure to keep and understand the most rudimentary records of MMEDs? We can envision no better argument for an "Alert and Communication Center" (which will be discussed later).

CARIBBEAN BLEACHING PATTERNS IN 1987

Once we accept increases in temperature as the probable cause of world-wide coral reef bleaching, then much of the variation can be explained. Reefs with large platforms, surrounded by shallows, or obstructed by physical structures which intensify poor circulation (Florida, the Bahamas, the Greater Antilles) bleached first and most intensely in 1987. These areas may have also experienced calmer conditions than the remainder of the western Atlantic during the period of most intense bleaching. Those with darkened waters to absorb solar heat (Islas del Rosario, Colombia; Florida Keys) or those prone to hypersaline formations (Bahamas, Florida Keys, Culebra, PR) bleached with particular intensity. Those with good circulation, narrow shelves, open ocean (Lesser Antilles, Curaçao, Bonaire, Bermuda) or those which did not experience calm conditions (Panama, Venezuela, Tobago, Trinidad and Tobago) took much longer to bleach, and experienced less bleaching. Bermuda did not experience any unusually high temperatures in 1987 and did not bleach. In 1988, high seawater temperatures accompanied coral reef bleaching there. The many reports of particular sides of islands or sides of reefs bleaching more intensely may be more easily understood if the efficiency of circulation is a factor.

WHY WORSE IN 1987 THAN 1983?

More extensive bleaching occurred in 1987 in the Caribbean and many parts of the Indo-Pacific during a modest ENSO event and fewer recorded SST anomalies, than in 1983 with a very severe ENSO event and more temperature anomalies. Overall, more bleaching occurred in more areas in 1987 than in 1983. We believe the 1987-88 event meterologically favored inshore temperature increases in more areas, also 1987 was a warmer year on average world-wide than 1983 (Kerr, 1988), deterioration of coral reefs was more advanced in 1987 and the resilience of coral reef hosts was less.

EASTERN PACIFIC 1983 AND 1987 COMPARISON

The eastern Pacific bleached less in 1987 than in 1983, while in most areas bleaching was more intense in 1987 than 1983. Possibly, the more sensitive hosts had already been killed in the eastern Pacific in 1983 and were not available to register bleaching in 1987. A better explanation may be

that reefs in the eastern Pacific are in areas that are less subject to inshore heating during calm conditions of the 1987 ENSO, or did not experience the calm conditions reported elsewhere. In contrast, the Florida Keys where bleaching is frequently correlated with ENSO events may be especially prone to indirect ENSO heating. The 1983 bleaching in the eastern Paific was through direct, overall seawater temperature increases, not just heating of inshore waters as in 1987. Quinn et al. (1987) classifies ENSO events to various strengths including "moderate", "strong", and "very strong". The bleaching related to direct heating may be associated only with very strong ENSO events, while the bleaching associated with calm conditions (indirect heating) may be associated with very strong to moderate ENSO events. Both types are devastating only because of the overall elevated background temperatures of the 1980's.

INDO-PACIFIC BLEACHING

The Indo-Pacific has many more coral reefs than the western Atlantic, but has a much lower density of coral reef scientists. Consequently, fewer reports were received from this region (Fig. 1). The low response might indicate few cases or less intense bleaching in these areas. However, the bleaching on the Great Barrier Reef was the most extensive and intense ever reported (Oliver PC, Zann PC) and the bleaching in the Maldives was intensive and extensive (Wood, 1988). Furthermore, the distribution of cases generally covers the entire region. We suspect that Indo-Pacific bleaching has been underreported. Other factors may have complicated the recognition of bleaching. In the eastern Pacific whole reefs were destroyed in 1983, and some coral species suffered extirpation (Glynn, 1984a; Glynn et al., 1989). Additional corals perished there in 1985 (Guzman et al., 1988) and the damaged reefs further eroded (Glynn, 1987) and suffered intense predation (Glynn, 1985a,b). There may be few hosts to bleach in some areas of the eastern Pacific. During the 1986-88 bleaching, new outbreaks of *Acanthaster planci* occurred on many Indo-Pacific reefs (Phillips, 1987). Their damage resembles bleaching and some bleaching may have gone unreported because it was attributed to *A. planci*.

FUTURE CORAL REEF BLEACHING

Limited histological examination suggests that photosymbiotic hosts cannot recover completely from bleaching in 2 years (Glynn and DeCroz, 1989). Since the period between main events has been 3-4 years and 2-3 years separate complexes, repeatedly bleached hosts would presumably fare worse with each bleaching bout. In past events, bleaching was sporatic and all geographic areas were not affected in each event. If future cycles become more widespread, there may not be sufficient time for complete recovery between local bleaching bouts and bleaching may become more devastating even with no increase in severity. This may have already happened in some areas (such as the Florida Keys) where bleaching occurred during all world-wide complexes. Examples of this problem can also be seen in the Gulf of California (Table 15) and Jamaica (Goreau PC) where more severe bleaching occurred 2 years after the 1987 event. Certainly these areas had not recovered from the intense 1987 bleaching.

If we are correct about temperature increases, the deterioration of the coral reefs, and ENSO events driving coral reef bleaching; then the upward spiral of bleaching damage in this cyclic process can only increase. All predictions indicate continued increases in temperature. All recent evaluations of coral reefs have found continuing and accelerating deterioration. We can find no evidence that either situation will stabilize or improve. Some variation is expected, but deterioration and temperture rises will continue and ENSO events are unlikely to cease. Coral reef bleaching complexes will probably increase in extent and severity.

If we have correctly identified the causes of bleaching, we can forsee this process causing increasing devastation to photosymbiotic hosts. Ultimately, we expect these hosts will no longer form a significant component of the former coral reef community and these systems will be profoundly different.

CONSEQUENCES

Cea-E. and DiSalvo (1982) and Gladfelter (1988) suggest that growth and carbonate productivity of bleached corals may be seriously reduced. Reese et al. (1988) found that while non-bleached

corals grew 2 mm of new skeleton, growth was not detectable in bleached and partially bleached colonies. The consequences of coral reef bleaching range from loss of energy of reef hosts for a few weeks to total replacement of the benthic community (Jaap, 1988). Following the 1983 event in the eastern Pacific, species suffered extirpation, whole reefs died, and bioeroders threaten to destroy the remaining reef structures (Glynn, 1987). Knowlton (1988) noted that Atlantic reefs are dominated by hosts whose life histories make rapid recovery from catastrophic mortalities very unlikely. Two of the most important, most rapidly growing reef-building corals in the Atlantic recently have been seriously reduced in abundance by WBD (Table 23). Buddemeier and Smith (1988) recently predicted the demise of coral reefs by rapidly rising sea level. Graus and Mcintyre (1988) used a computer model to show that no Caribbean reefs will keep pace with the predicted sea level rise, higher waves will resuspend previously deposited sediment, and some entire reefs may die. They assumed that growth of *Acropora palmata* and *A. cervicornis* may keep pace with sealevel rise in the beginning, but they did not consider the WBD damage these corals are suffering. The increases in temperature associated with the "greenhouse effect" may destroy the reefs before they can drown. If temperature increases are causing the world-wide coral reef bleaching events, it may be a preview of what problems even small increases can cause (Wicklund in Hollings, 1988). Loss of much of the coral reefs may futher accelerate the "greenhouse" process. Coral reefs form an important buffer in the global carbon dioxide cycle (Lang in Hollings, 1988; Buddemeier, 1989), as calcium carbonate is one of the most important reservoirs of atmospheric carbon dioxide (Ohde, 1988).

All of the changes in the environment of coral reefs appear to be impacts caused by humans. Sedimentation, nutrification and pollution through direct human actions; increased seawater temperatures and sealevel rising, and possible UV light, through atmospheric additions. Other major marine ecological disturbances (Table 23) may also be related to these human impacts. Modification of human activities to cease or moderate these processes is probably physically possible, but the probability of this happening is low because the political and economic costs are so great.

Grigg (1989) suggests that coral reefs are "robust" ecosystems which have overcome the effects of rapid sealevel rise and other negative effects in the past and will do so in the future. It has been suggested (Jackson and Hughes, 1985) that drastic damage to coral reefs in the past has led to increased diversity of species on the reefs and aided in the success of the system. In those times, impacts were simple and direct, while the present ones are multiple and complex. Past damage occurred in a healthy system, while the present system seems already to be showing signs of deterioration.

If global temperatures continue gradually increasing, then extensive coral reef bleaching will eventually occur during every warmwater period in much of the tropics without aid of ENSO warming events. Whether most coral reef hosts in these areas survive until overall SST increases to that point depends on the severity and frequency of ENSO warming. The temperature increases should make portions of the former temperate zones more temperature-suitable for hosts as portions of the tropics become too hot for them. Unfortunately, the temperate zones are too high in nutrients to be suitable for most hosts (which require nutrient poor waters). These increases will also be accompanied by coastal flooding (Buddemeier and Smith, 1988) which will produce nutrient levels and sedimentation in almost all coastal areas detrimental to host growth and survival (Hallock and Schlager, 1986). ENSO warming may be providing a preview of the effects that increasing temperatures and increasing deterioration will have on coral reefs. The fragile coral reefs, in turn, may be providing a preview of more widespread disturbances.

RELATED MAJOR MARINE ECOLOGICAL DISTURBANCES

Major marine ecological disturbances have recently increased in number and severity both regionally (Phillips, 1987; Williams, E. and Williams, 1987; Birkeland, 1989; Table 23) and globally (Birkland and Eldredge, 1988; Sindermann, 1988; Williams and Bunkley-W., 1988, 1989; White, 1989; Table 23). Some of the increase in number of reports could be due to increased number of observers (Birkland and Eldredge, 1988) or an increased awareness of the problem, but most of these disturbances are too obvious to have been previously ignored. Disturbances are spreading to new geographic areas (Bonaventura and Bonaventura, 1988; Tester, 1988; White, 1988, 1989) and wholely new or unknown diseases are erupting (Anonymous, 1989; Bird and Wright, 1989). Many of these disturbances share the quasi-synchronous timing, complexity, and high variation of the coral reef bleaching events (Phillips, 1987; Williams, E. and Williams, 1987; Sindermann, 1988; Williams and

Table 23: Other Recent Major Marine Ecological Disturbances.[1]

DATE	ORGANISM AFFECTED	LOCALITY	SOURCE
Since mid-1800's	Mass fish kills (red tide) (*Ptychodiscus brevis*)	Gulf of Mexico	White 1988
Since 1900, but more common in recent years(?)	Crustacean shell disease syndrome	World-wide high incidence in crowded or degraded habitats	Sindermann 1989
Since mid-1960's	Mass kills of fishes (*Gyrodinium aureolum*)(red tide)	Europe	White 1988
1965	Mass shelfish and fish kills (*Gyrodinium aureolum*)(red tide)	Omura Bay, Japan	White 1988
1966, 1976, 1981, 1982	Caged and wild fishes and invertebrates (red tide) (*Gyrodinium aureolum*)	Norwegian Coast	White 1988
1969 - present	Chronic outbreaks (*Acanthaster planci*)	Ryukyu Islands	Yamaguchi 1986 Birkeland 1989
1969 - present	Red tides spreading and increasing in frequency	World-wide	White 1989
1970 - 1985	Cultured yellowtail mortalities (*Chattonella antiqua*)(red tide)	Japan	White 1988
July 1973	Mass kill of cultured fishes (*Heterosigma akashino*)(red tide)	Ireland	White 1988
Mostly mid- to late 1970's to present	Ulcerative diseases in coastal/esturine fishes	World-wide	Sinderman 1988
1975 - present	Red tides, dinoflagellate blooms and paralytic shellfish poisoning increasing at a geometric rate	western Pacific	Birkeland 1989 Holmes and Catherine 1985 McClean 1984
1976, 1979	Mass mortality of Atlantic herring (*Gonyaulax excavata*)(red tide)	Bay of Fundy, Canada	White 1988
1977	Outbreak and severe damage by *Acanthaster planci*	American Samoa	Kluge-E. PC
1977 - present	Coral mass mortality (*Acropora cervicornis*)	Greater Caribbean Region	Carpenter in Hollings 1988
1978	Mass mortality of sand lance (paralytic shellfish toxins)	Cape Cod, Massachusetts	White 1988

Summer 1978	Sea star mass mortality (*Heliaster kubiniji*, *Othilia tenuispina*)	Gulf of California	Dugan et al. 1982
August 1978	Sponge mass mortality (*Xestospongia muta*)	Florida Keys, USA	Causey PC
Summer 1978 Summer 1979	Mass mortality of sea stars, sea cucumbers (*Piaster* spp., *Patiria miniata*, *Stichopus parvimensis*)	southern California	Dugan et al. 1982
1978 - present	Diarrheic shellfish poisoning	World-wide	White 1988
1979	Menhaden kill (red tide) (*Gonyaulax excavata*)	Maine	White 1988
1979, 1982	Mass kill of cultured fishes (*Heterosigma akashino*)(red tide)	western Scotland	White 1988
1979 - present	Chronic outbreaks *Acanthaster planci*	Guam	Birkeland 1989
1979 - present	widespread death of *Acropora palmata* and *Porites porites*	Anegada, British Virgin Islands	Brown 1987
1979 - present	Frequency of algal (red tide) blooms in North Sea increases over the last 10 years	North Sea	Saunders 1988
1979 - present	Isolated incidences of coral reef bleaching of shallow symbiotic hosts	Ko Phuket, Thailand	Brown 1987
1980	Caribbean-wide fish kill	Caribbean, Bahamas, Florida (USA)	Williams, E. & Williams 1987
1980	Mass mortality of anchovies (*Engraulis mordax*)	Santa Cruz Harbor California, USA	Friedman 1989
1980	Fish kill (red tide) (*Gyrodinium aureolum*)	Scotland	White 1988
1980 - present	Series of red tides	Hong Kong	Wu 1988
Early 1980's	Eelgrass wasting disease	New Hampshire and Maine, USA	Short et al. 1986
1981	Mass kill of "sardine-like" species (*Harengula*??)	Venezuelan coast	Atwood PC
1981	Diadematid urchin mass mortality	Hawaiian Islands	Birkland & Eldredge 1988 Choquette PC, Hau PC

1981	Mass kill of cultured fishes (*Heterosigma akashino*)(red tide)	Inland Sea of Japan	White 1988
Summer 1982?	Coastal fishes mass mortality	Venezuela	Newspaper
Summer 1983	Sponge mortalities	South Florida, USA	Causey PC
Summer 1983	Mortalities of fish and shellfish (*Prymnesium calthiferum*)	New Zealand	White 1988
1983 - 1984	Sea urchin mass mortality (*Diadema antillarum*)	Wider Caribbean	Lessios et al. 1984 Lessios 1988b
1983 - present	Mass mortality of sea fans (*Gorgonia* spp.)	Costa Rica Panama, Colombia	Guzman 1984, Guzman PC
1983 - present	Population reduction (*Crassostrea virginica*)	Gulf of Mexico, Mississippi coast	Newspaper
1983 - present	Mysterous ailment of loons (*Gavia immer*)	Gulf and Atlantic coasts of Florida, USA	McIntyre 1989
1984	Mass mortality of anchovies, (*Engraulis mordax*)	Santa Cruz Harbor California, USA	Friedman 1989
July 1984, 1985, 1987	Kills of farmed fish (red tide)(*Gonyaulax excavata*)	Faroe Islands	White 1988
December 1984	Sea urchin mortality (*Astropyga magnifica*)	Puerto Rico	Williams et al. 1986
1984, 1985	Mass kills of caged fish (*Gyrodinium aureolum*)(red tide)	Inland Sea of Japan	White 1988
1985-1986 1987	Giant Clam mass mortality	Great Barrier Reef, Australia	Goggin & Lester 1988; Alder & Braley 1989
January 1985	Sea urchin mortality (*Eucidaris tribuloides*)	Puerto Rico	Williams et al. 1986
1985	Coral mortalities due to red tide	Eastern Pacific	Guzman et al. 1988
1985	Pearl and Mother-of-pearl oyster mass mortality	Tuamotu Archipelago French Polynesia	Birkland & Eldridge 1988 Intes 1988
June 1985, May-June 1986	Mass mortalities of herring	Alaska	Meyer 1989

Summers from 1985 - present?	Brown Tide Mortalities mussels and scallops (*Aureococcus anophagefferens*)	Narragansett Bay Long Island Bays	Anonymous 1989 Bricelj 1987
August 1985	Fish mass mortality (*Harengula* spp.)	Puerto Rico	This paper
October 1985	Secondary die-off (*Diadema antillarum*)	St. Croix	Lessios 1988b
November-December 1985	Secondary die-off (*Diadema antillarum*)	Panama	Lessios 1988b
1985 - 1986	MSX epizootic in oysters (*Haplosporidium nelsoni)*	east coast USA	Haskin 1987
1985 - present	Clam mass mortalities (*Perkinsus atlanticus*)	Portugal	Azevedo 1989
1986	Fish and shellfish kills (red tide)(*Ptychodiscus brevis*)	Texas (worst ever in Gulf of Mexico)	White 1988
June 1986	Mass mortality of sea urchins (*Echinometra mathaei*)	Okinawa	Tsuchiya et al. 1987
June 1986	Mass kill of cultured fishes (*Heterosigma akashino*)(red tide)	British Colombia	White 1988
1986 - 1989	50 beluga whales immuno-deficiency	St. Lawrence River	Goodavage 1989
August 1986 - present?	Sponge epizootic (*Hippospongia communis*)	eastern Mediterranean Tunisia, Greese, Turkey, Cyprus	Reiswig 1988 Vicente 1989
October 1986	Massive fish kill	Texas, USA; Mexico	Associated Press 1986
1987 - 1989	Distemper epizootic and mass mortalities of seals	Lake Baikal, USSR	Clapham & Baraff 1989
June 1987 - March 1988	Bottlenose dolphin mass mortality	Atlantic coast of U.S. New Jersey to Florida	Segars 1987 Hollings 1988 NOAA 1989 Scott et al. 1988 Geraci 1989
Summer 1987	"Enormous" fish kill	Long Island Sound USA	Hollings 1988
Summer 1987	Shellfish kill, fish kill	Long Island Sound USA	Van Patten 1989
Summer 1987	Sponge mortalities	south Florida, USA	Causey PC

Summer 1987	Mass mortality, commercial oyster (MSX, *Haplosporidium nelsoni*)	Massachusetts to Georgia, USA	Fritz & McVey 1989
August - September 1987	Epizootic of black band disease	Florida Keys, USA	Causey PC
Summer-fall 1987	Sea grass blight	south Florida, USA	Tasker 1988
Fall 1987	Mass mortality of fishes	Norway	
Fall 1987	Humpback and Minke Whale die-off (red tide)	New England, USA	White 1989
Fall 1987	Fish kills (*Harengula* spp.)	St. Kitts/Nevis	This paper
November 1987 - July 1988??	Abalone mortality (black, red, pink, & green abalone)	California, USA	Richards 1988
Autumn/Winter 1987	Amnesic shellfish poisoning and massive diatom bloom (*Nitzschia pungens*)	Canada, but possibly a world-wide problem	Bird and Wright 1989
September 1987 - February 1988	Massive red tide (*Ptychodiscus brevis*)	North Carolina	Bonaventura & Bonaventura 1988 Tester 1988
January 1988	Worst red tide in 10 year series (*Gonyaulax polygramma*)	Hong Kong	Wu 1988
1988	Red tides increasing in frequency	Kuwait	Linden in Jeftic et al. 1988
1988	7,000 harbor seals distemper epizootic	North Sea	Goodavage 1989
1988? - Present	Eelgrass wasting disease	North America & Europe	Muehlstein PC
1988 - Present	Blue-green algae overgrowth of turtlegrass	US and British Virgin Islands	Muehlstein PC
Mid May - mid June 1988	Mass mortality (red tide) (*Chrysochromulina polylepis*)	Norway	Saunders 1988
Summer-fall 1988	Sea grass blight	south Florida, USA	Tasker 1988
Winter 1988	Fish Kills (*Harengula* spp.)	St. Kitts/Nevis	This paper

Late 1988	Amnesic shellfish poisoning and massive diatom bloom (*Nitzschia pungens*)	Canada, but possibly a world-wide problem	Bird and Wright 1989
January - March 1989	Brown pelican mortality	Puerto Rico and US Virgin Islands	This paper
May 1989	Fish Mass Mortality (*Harengula* spp.)	St. Vicent	Sealy PC
June 1989	Fish Mass Mortality (*Harengula* spp.)	Barbados	Sealy PC
Recent	Epidemics [sic] of tumors in soft-shell clams	Massachusets, USA	Smolowitz 1987
In recent years	Disturbing spread of paralytic shellfish poisoning	Worldwide	White 1988
?	Mass mortality (*Acropora cervicornis*)	San Blas Islands Panama	Knowlton et al. 1988
?	*Acanthaster planci* outbreaks	Australia	Zann & Moran 1988 Endean 1982 Walton 1984
?	Coralivorus gastropod outbreak (*Drupella* sp.)	Miyake-jima (Japan) Phillipines western Australia	Birkland & Eldridge 1988
?	Mass sponge mortality (*Chondrilla nucula*)	Puerto Rico	Vicente 1989
?	Black band disease *Pseudopterogorgia acerosa*, *P. americana*)	Florida Keys, USA	Feingold 1988

[1]This table does not represent an exhaustive search for major marine ecological disturbances, only those that came to the attention of the authors during the bleaching study. Most marine mortalities go unreported.

Bunkley-W., 1988, 1989; Table 23), and many of these events were first noticed in the late 1970's or early 1980's (Brown, 1987; Sindermann, 1988; Table 1). The possibility of relationships and shared causes among these events requires examination.

ALERT AND COMUNICATION CENTER AND NETWORKS

The bleaching episodes of 1979, 1980, 1982, 1983 and 1986 were not immediately recognized as parts of world-wide, circumtropical events because no agency was looking for large scale events. Many of the reports of bleaching in locations other than the eastern Pacific that were published by Glynn (1984a,b) were sent to him unsolicited (Glynn, 1984a). No comprehensive attempt was made to follow these events. Other reports of bleaching, with the exception of Brown (1987), were largely of local events. Major marine ecological disturbances are often misidentified and understudied as local, disjunct events. Possibly, a first step toward recognizing and dealing with large scale events would be an "Alert and Communications Center" where major marine ecological disturbances could be recorded, similar reports collated, and summaries issued. A similar system has been established

to follow red tides by Sea Grant and the Woods Hole Oceanographic Institution (White, 1989). A network to follow marine mammal strandings in North America has existed at the Smithsonian Institution since 1975 as the "Scientific Events Alert Network" (1975-1982) and the "Marine Mammal Events Program" (1982-present). A similar program has been proposed in Europe (Cousteau, 1984).

Some time in the late 1970's, 2 of the principal reef-building corals in the shallow Atlantic coral reefs began to die. This mass mortality continued until the majority of *Acropora cervicornis* in the region was destroyed (Carpenter in Hollings, 1988) and *A. palmata* was severely affected. In 1980, fishes died throughout the tropical and subtropical western Atlantic. The disturbance lasted for months and millions of fishes perished (Williams et al., 1982; Atwood, 1984; Williams, E. and Williams, 1987). In 1981, a mass mortality of diadematid sea urchins occurred in the Hawaiian Islands (Choquette PC; Hau PC). We are unaware of any attempts made to follow, document or study these major events. The 1983 greater Caribbean-wide *Diadema antillarum* mass mortality was well followed and documented by Lessios et al. (1983, 1984) and Lessios (1988), the 1982-83 world-wide coral reef bleaching event was followed by Glynn (1984a,b), and the world-wide epizootic ulcerative syndromes of fishes was reviewed by Sindermann (1988), but none of these events has been studied in sufficient detail. No causes have been assigned. Many other related events (Table 23) are probably more serious and widespread than the limited available data suggest. Studies of coral reef host diseases have not been fundable (Shinn, 1989). A recent proposal to examine the MMED of sponges in the mediterranean failed to obtain support (Reutzler PC) and a recent study of white band disease was underfunded to the point of leaving the etiology of the disease unexamined (Peters PC). The recent review of the MMED of *Diadema antillarum* (Lessios, 1988) shows that much work has been accomplished on the ecological aftermath of this epizootic, but nothing is known about the disease. Examination of these diseases may be critical to our understanding of coral reef deterioration and possibly other related largescale MMEDs (Table 23).

The number, complexity, extent and severity of these disturbances is alarming. Our lack of understanding and documentation of the events is a cause for concern. Glynn (1984a), Birkland and Eldredge (1988), Sindermann (1988) and Ogden (1989) have called for more rapid and comprehensive investigation of regional and global MMEDs. We suggest that an Alert and Communications Center (ACC) would be the most inexpensive, elemental and basic start toward confronting these serious disturbances. A simple, but continuing, ACC could provide: (1) Early detection of each event through a "Hot-line" and a communication network for existing field biologists; (2) Confirmation of the extent of the problem by appropriate members of a field network; (3) Study of the event by existing scientists in unaffiliated laboratories who can quickly be notified of a potential disturbance; (4) Communication of progress through summaries based on questionnaires in cooperation with unaffiliated experts. The ACC would function largely with existing field scientists and existing experts who would appreciate and would act upon timely information about major marine ecological disturbances. This useful system could replace the former disarray and dismay in dealing with these major events (Williams, E. and Williams, 1987).

Most information about a major marine ecological disturbance is only available while the event is occurring. Once a disturbance ceases, both interest in reporting the event and the reliability of memory decline. The bulk of the data we obtained to understand the patterns of bleaching in 1986-88, left unrecorded, would have essentially ceased to exist. Without an Alert and Communication Center-type effort, large-scale coral reef bleaching would have remained a mysterious event.

We hope our limited efforts to follow the 1986-88 coral reef bleaching events suggest what more could be accomplished with a permanent, well advertized, Alert and Communication Center. A Center, which would have been called in mid-June 1987 about the impending bleaching event and mortalities in the Florida Keys (Causey PC), could have alerted coral reef scientists then instead of in late October (as actually happened). A Center would not only have been contacted about the 1986 events, but may have been able to accurately predict the 1987-88 event 1 year in advance [whether the model (Fig. 4) is accurate or not, it would, in this case, have made a correct prediction in 1986]. Fisheries biologists in many areas of the Caribbean would not be investigating possibly related mass mortalities of the same species of fish as isolated events (Table 23). Dozens of biologists, who have studied the 1983-84 mass mortalities of *Diadema antillarum* and the effects on Caribbean reefs (Lessios, 1988), would not have been unaware of a similar mass mortality of diadematids which occurred in the Hawaiian Islands in 1981 (Table 23). The discovery of a virus causing a mass mortality of pearl oysters (Birkeland and Eldredge, 1988) would be known to researchers reporting no pathogenic vector for apparently the same event 4 months later (Intes, 1988) (Table 23). And

many more pieces (which are now being lost) of each puzzle would be made available for those who seek to solve these problems.

We believe we have found sufficient correlations to implicate the causes of the recent world-wide coral reef bleaching events by using the techniques that would be employed by an Alert and Communications Center. We hope this concept can be used to follow other important MMEDs.

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APPENDIX 1. The following questionnaire, or a similar version (there were several versions that were sent out by us or reprinted in other publications) was used to gather the information used to make this report. This form may also be used for additional reports to us about coral reef bleaching or mortalities.

CORAL AND OTHER COELENTERATES AND SPONGES BLEACHING AND MORTALITIES QUESTIONNAIRE

Department of Marine Sciences, Caribbean Aquatic Animal Health Project, University of Puerto Rico, P.O. Box 579 or 908, Lajas, PR 00667
Telephone (809) 899-2048. Telex: UPR MAY 3452024. FAX: 809-265-2880

Please complete and return as soon as possible. Save or xerox an extra copy to report more than one geographic location, for future observations, or to send to other observers. If an answer requires more space, use the question number, and continue your answer on another sheet of paper. Thank you.

NAME: TELEPHONE NUMBER(S):
ADDRESS:
TELEX:
FAX:

DATE OF OBSERVATIONS: DATE QUESTIONNAIRE COMPLETED:

1. Circle the groups which bleached: Stony corals; Fire Corals; Soft corals; Zoanthids; Anemones; Hydroids; Sponges; Mollusks; ____________.

   Please also complete the following form if possible.

SPECIES BLEACHED	NUMBER SEEN	NUMBER BLEACHED	% SURFACE BLEACHED

2. What percentage of the total area of all living corals in a geographic area were bleached ?

3. Were there patterns of bleaching within geographic areas or habitats?

4. What geographic areas were involved?

5. At what depths did the bleaching occur?

6. What animals (closely related to those that were bleached) were not bleached?

7. When did the bleaching start?

8. What bleached first? What bleached last?

9. What recovered first? What recovered last?

10. When did recovery begin?

11. How long did it take for the bleaching to occur? Days? Weeks? Months?

12. How many whole colonies died? How many suffered partial necrosis?

13. Did mortalities occur during the bleaching? After the bleaching?

14. What do you think caused the bleaching?

15. What bleaching events have occurred before in your geographic area?

16. How do past bleachings compare with the present bleaching?

17. Did more or less bleaching occur in particular habitats or situations?

18. When did the bleaching become the worst or the most extensive?

19. Was geographic spreading of this event observed?

20. Were any unusual physical or meterological events noted before or during the bleaching?

21. Were temperatures and/or other measurements taken at the surface and/or at depth during and/or before the bleaching?

22. Besides the bleached coelenterates and sponges, were any other animals and/or plants noted damaged or killed during the bleaching event?

23. Did anything else out of the ordinary occur during the bleaching?

24. Please add any additional comments or information which you feel are pertinent.

25. What other topics should have been included in this (and future) CAAHP questionnaires?

Thank you very much for this valuable information. Everyone who responds will receive summaries of the information as it becomes available.

APPENDIX 2: Classification and authors of names used. Phyla follow Margulis and Schwartz (1988)

I. Kingdom Prokaryote - Bacteria
- Phylum Cyanobacteria - Blue-green algae
  - "cyanobacteria"
  - Class Oscillatoriaceae
    - Order Oscillatoriales
      - *Phormidium corallyticum* Ruetzler and Santavy
- Phylum Pseudomonadia(?)
  - "bacteria"
- Phylum Omnibacteria(?)
  - "bacteria"

II. Kingdom Protoctista
- Phylum Dinoflagellata - Dinoflagellates
  - "dinoflagellate"
  - *Gonyaulax polygramma*
  - *Gonyaulax excavata*
  - *Gyrodinium aureolum*
  - *Ptychodiscus brevis* (Davis)
  - "zooxanthellae"
- Phylum Haptophyta
  - *Chrysochromulina polylepis*
  - *Prymnesium calithiferum*
- Phylum Chrysophyta
  - Class Raphidomonadales
    - *Aureococcus anophagefferens*(?)
    - *Chattonella antiqua*
    - *Heterosigma akashino*
- Phylum Bacillariophyta - Diatoms
  - *Nitzschia pungens*
- Phylum Rhodophyta - Red Algae
  - "red algae"
  - Class Corallinaceae
    - Order Corallinales
      - "coralline algae"
- Phylum Ciliophora - Ciliates
  - "ciliate"
- Phylum Apicomplexa
  - Class Perkinsea
    - Order Perkinsida
      - "perkinsid"
      - *Perkinsus atlanticus* Azevedo
      - *Perkinsus* sp.
  - Class Sporozoasida
    - Order Coccidida
      - "coccidian"
    - Order Haplosporida
      - *Haplosporidium nelsoni* (Haskin, Stauber and Mackin)

III. Kingdom Fungi - Fungi
- "fungi"

IV. Kingdom Animalia - Animals
Phylum Porifera - Sponges
"unidentified sponges"
Class Demospongiae
Order Homosclerophorida
Plakortis sp.
Order Carnosa
Chondrilla nucula Schmidt
Order Halichondriida
Hymeniacidon sp.
Order Hadromerida
Anthosigmella varians (Duchassaing and Michelotti)
Cliona aprica Pang
Order Haplosclerida
Xestospongia muta (Schmidt)
Order Poeciloscierida
Agelas conifer (Schmidt)
Mycale laevis (Carter)
Order Dictyoceratida
Hippospongia communis Linnaeus
Phylum Cnidaria - Corals and allies
"cnidarians"
Class Hydrozoa
"hydrozoans"
Order Milleporina - Fire corals
Millepora alcicornis Linnaeus
Millepora complanata Lamarck
Millepora dichotoma Vaughan
Millepora platyphylla Ehrenberg
Millepora sp.
Order Stylasterina - Stylaster corals
Stylaster roseus (Pallas)
Class Anthozoa
"anthozoid"
"anthozoan"
Order Helioporacea - Blue coral
Heliopora coerulea (Pallus)
Order Alcyonacea - Soft corals
"alcyonarians"
Cladiella sp.
Lobophytum sp.
Order Gorgonacea - Gorgonians
"unidentified soft corals"
Briarium asbestinum (Pallas)
Eunicia sp.
Iciligorgia schrammi Duchassaing
Gorgonia sp.
Pseudopterogorgia acerosa (Pallas)
Pseudopterogorgia americana (Gmelin)
Order Actiniaria - Sea Anemones
"unidentified anemones"
Stoichactis helianthis (Ellis)
Order Corallimorpharia - Coral-like anemones
Ricordia florida (Duchassaing and Michelotti
Order Zoanthidea - Zooanthids
Palythoa caribbea Duchassaing
Palythoa mammilosa (Ellis and Solander)

Palythoa tuberculosa Esper
Order Scleractinia - stony corals
Acropora cervicornis (Lamarck)
Acropora palmata (Lamarck)
Acropora sp.
"acroporids"
Agaricia agaricites (Linnaeus)
Agaricia lamarcki Milne-Edwards and Haime
Agaricia sp.
Colpophyllia natans (Muller)
Colpophyllia sp.
Dendrogyra cylindricus Ehrenberg
Diploastrea heliopora (Lamarck)
Diploastrea sp.
Diploria clivosa (Ellis and Solander)
Diploria labyrinthiformis (Linnaeus)
Diploria strigosa (Dana)
Diploria sp.
Eusmilia fastigiata (Pallas)
"Faviids"
Favia fragum (Esper)
Favia sp.
Favites sp.
Fungia sp.
Goniastrea sp.
Leptoseris sp.
Meandrina meandrites (Linnaeus)
Montastrea annularis (Ellis and Solander)
Montastrea cavernosa (Linneaus)
Montipora sp.
Mycetophyllia lamarckiana Milne-Edwards
Oculina varicosa Lesueur
Pavona clivosa Verrill
Pavona gigantea Verrill
Pavona sp.
Platygyra sp.
Pocillopora damicornis (Linnaeus)
Pocillopora elegans Dana
Pocillopora meandrina Dana
Pocillopora verrucosa (Ellis and Solander)
Pocillopora sp.
Porites astreoides Lesueur
Porites californica Verrill
Porites lobata Dana
Porites porites (Pallas)
Porites sp.
Psammocora stellata Verrill
Seriatopora hystrix Dana
Siderastrea radians (Pallas)
Siderastrea siderea (Ellis and Solander)
Siderastrea sp.
Solenastrea bournoni Milne-Edwards and Haime
Stylophora pistillata Esper
Stylophora sp.
Symphyllia sp.
Order Antipatharia - Black corals
"black coral"

Phylum Ectoprocta - Bryozoans
"bryozoans"
Phylum Mollusca - Mollusks
"mollusk"
Class Gastropoda - Univalves
"gastropod"
Order Archaeogastropoda
"black, red, pink, green abalone"
Order Mesogastropoda
Drupella sp.
Revitrona caputserpentis (Linnaeus)
Strombus gigas Linnaeus
Class Pelecypoda - Bivalves
Order Filibranchia
Argopecten irradians (Lamarck)
Crassostrea virginica (Gmelin)
"mussels"
Mya arenaria Linnaeus
Mytilus edulis Linnaeus
"scallops"
Order Eulamellibranchia
Chama sp.
Tridacna gigas Linnaeus
Tridacna sp.
Phylum Annelida
Class Polychaeta - Polychaete worms
"polychaete"
Phylum Echinodermata - Echinoderms
"echinoderms"
Class Asteroidea - Sea stars
Order Spinulosa
Acanthaster planci (Linnaeus)
Othilia tenuispina Verrill
Patiria (=Asterina) miniata Brandt
Order Forcipulata
Heliaster kubinijii Xantus
Piaster sp.
Class Echinoidea - Sea urchins, sand dollars
"echinoderms"
Order Cidaroidea
"urchins"
Astropyga magnifica Clark
Diadema antillarum Phillipi
"diadematid urchins"
Echinometra mathaei (de Blainville)
Eucidaris tribuloides Lamarck
Tripneustes ventricosus (Lamarck)
Class Holothurioidea - Sea cucumbers
Order Aspidochirota
Stichopus parvimensis (Clark)
Stichopus sp.

Phylum Chordata - Chordates
- Class Ascidiacea - sea squirts
  - "tunicates"
- Class Osteichthys - Bony fishes
  - "fishes"
  - Order Anguilliformes
    - "moray eels"
  - Order Clupeiformes
    - *Brevoortia tyrannus* (Latrobe)
    - *Clupea harengus* Linnaeus
    - *Harengula* sp.
    - "herring"
    - *Engraulis mordax* Girard
  - Order Gasterosteiformes
    - "trumpetfish"
  - Order Perciformes
    - "anemonefish"
    - *Ammodytes americanus* DeKay
    - *Seriola quinqueradiata* Temminck and Schlegel
- Class Aves - Birds
  - Order Pelecaniformes - Pelecans
    - *Pelecanus occidentalis*
  - Order Gaviiformes - Loons
    - *Gavia immer*
- Class Mammalia - mammals
  - Order Carnivora
    - *Phoca sibirica* Gmelin
    - *Phoca vitulina* Linnaeus
  - Order Cetacea
    - *Balaenoptera acutorostrata* Lacepede
    - *Delphinapterus leucas* (Pallas)
    - *Megaptera novaeangliae* (Borowski)
    - *Tursiops truncatus* (Montagu)

V. Kingdom Plantae - Plants

Phylum Angiospermophyta
- Class Hydrocheritaceae
  - Order Butomales
    - *Thalassia testudinum* Koenig
    - "sea grasses"
    - *Zostera marina* Linnaeus

ATOLL RESEARCH BULLETIN

NO. 336

BUCK ISLAND BAR, ST. CROIX, USVI: A REEF THAT CANNOT CATCH UP WITH SEA LEVEL

BY

IAN G. MACINTYRE AND WALTER H. ADEY

ISSUED BY
NATIONAL MUSEUM OF NATURAL HISTORY
SMITHSONIAN INSTITUTION
WASHINGTON, D.C., U.S.A.
January 1990

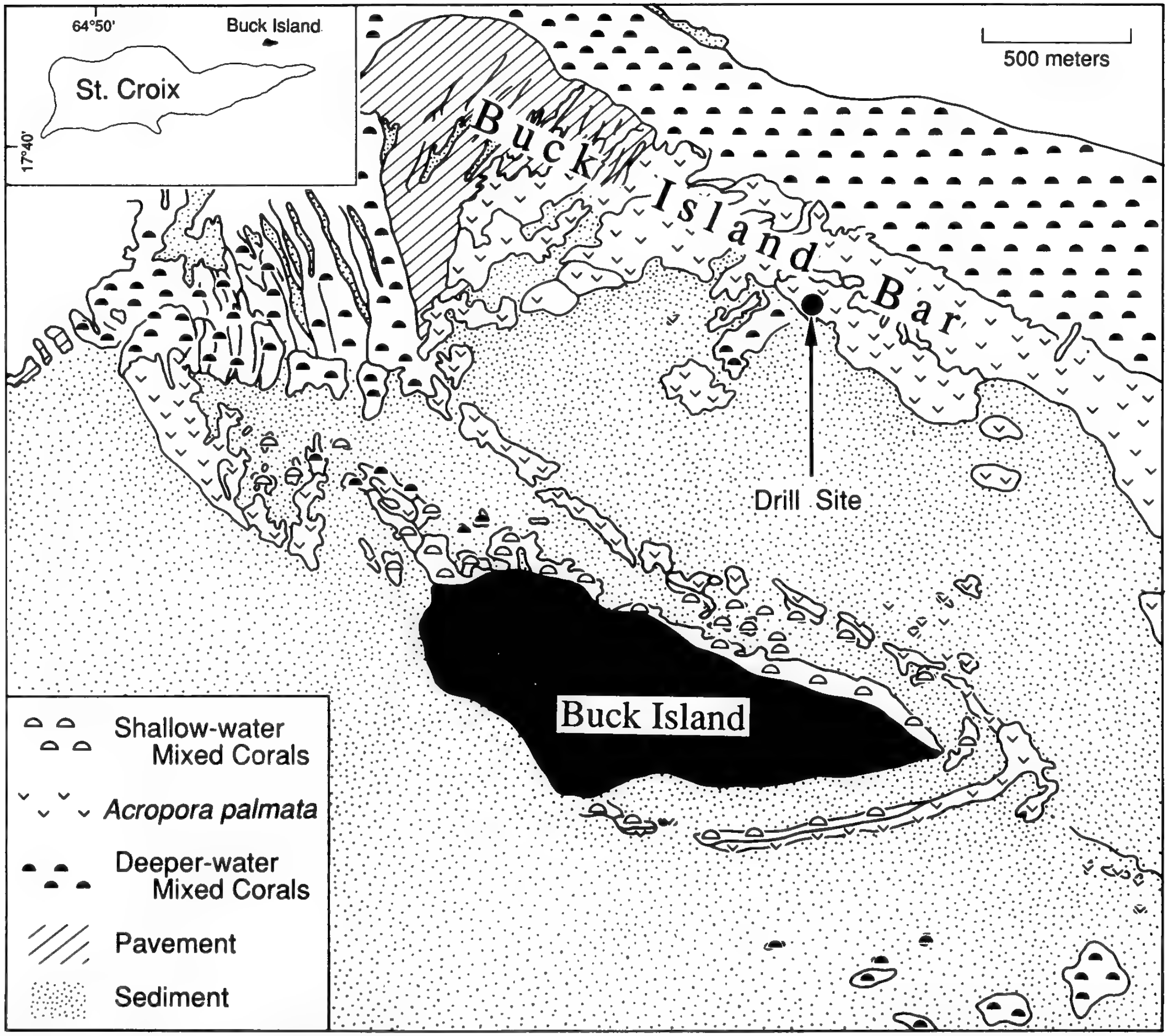

Fig. 1. Index map showing the general zonation of the sea floor around Buck Island and the location of the drill site on Buck Island Bar, near the outer edge of the shelf.

BUCK ISLAND BAR, ST. CROIX, USVI:

A REEF THAT CANNOT CATCH UP WITH SEA LEVEL

BY

IAN G. MACINTYRE AND WALTER H. ADEY

ABSTRACT

Frequent storms have disrupted reef growth on Buck Island Bar at the shelf edge off the north coast of St. Croix, U.S. Virgin Islands and have prevented the reef from catching up with the rising seas of the Holocene Transgression. An 8-m-long core hole in this reef indicates that Acropora palmata has been established here for over 4,000 years. Although this branching coral is capable of growing at rates in excess of 10 m/1,000 years, extratropical swell and perhaps hurricane damage have limited framework accumulation, and the remaining geological record is dominated by massive coral heads and well-lithified bare pavements.

INTRODUCTION

Holocene coral reef frameworks up to 18 m thick have been documented from numerous localities in the eastern Caribbean (Adey and Burke, 1976). The shallow inshore reefs on the north side of St. Croix (where they are protected by Buck Island and associated reefs) and on the south side are capped by an extensive framework of Acropora palmata, a rapidly growing and robust coral. As a result, framework construction has exceeded the rate of late Holocene sea-level rise (Adey, 1975), and reef flats are common in these areas. A submerged coral reef also exists on a raised edge of the shelf along the north coast of Buck Island and extends around the entire east coast of St. Croix.

The purpose of our project was to obtain a deep core from the early Holocene framework and to establish a relationship between these shelf-edge reefs and the inshore bank-barrier reefs. In November 1977, we drilled a hole into the reef at Buck Island Bar, near the shelf edge north of Buck Island (Fig. 1). This proved to be a difficult undertaking as we had to work at a depth of 5.18 m among thickets of Acropora palmata (Fig. 2) during heavy swells. These conditions prevented us from drilling much deeper than 8 m. Despite these drawbacks, we obtained

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Fig. 2. Buck Island Bar drill site. Note the abundance of the branching coral Acropora palmata. Water depth 5.18 m.

valuable data that have shed additional light on the history of the Holocene reefs of St. Croix.

DESCRIPTION OF THE STUDY SITE

The map showing the location of the core hole (Fig. 1) was constructed from 1976 to 1979 by P. J. Curry and W. H. Adey from color positives of a 1971 aerial survey and was validated by numerous underwater observations. For a detailed description of the coral reefs and algal ridges off St. Croix, see Adey (1975).

We selected a drill site in an Acropora palmata community toward the outer edge of the shelf north of Buck Island. On naval charts this raised part of the shelf edge is identified as Buck Island Bar (U.S. Coast and Geodetic Survey Chart # 905). This shallower section of the shelf-edge reef system occurs at an average depth of about 4 m, but a few thickets of A. palmata extend to within 0.5 m of the water surface. The reef site is separated from the shallow bank-barrier and fringing reefs of Buck Island by a sandy shelf up to 14 m deep (Fig. 1).

SUBSURFACE DATA

A hydraulically powered drill designed for underwater operation (Macintyre, 1975; Fig. 2) was used to penetrate to a total depth of 8.21 m in five intervals (Fig. 3). The first core-hole interval (0-1.68 m) consists of mixed heads of Diploria sp., Porites astreoides, Montastrea annularis, and branching Acropora palmata, all of which exhibit patches of micrite cement crusts and infillings of submarine Mg-calcite.

This upper interval also contains two sections of well-lithified pavement limestone--one at a depth of 1 m, and the other at the base of the core interval--consisting of heavily cemented coral heads and Millepora sp. This limestone is similar to that found in other parts of the Caribbean, which is usually an agglomeration of high-energy reef components, including crustose coralline algae, Millepora sp., Porites astreoides, and Agaricia agaricites (Macintyre 1977), with a diagenetic matrix of micritic Mg-calcite that "completely infills most of the inter- and intraparticle pore space to form a marble-like limestone" (Macintyre and Marshall, in press). Much of the original skeletal material has been lost during multicyclic stages of boring, infilling, and lithification.

The next two intervals, to a depth of 4.19 m, are dominated by Montastrea annularis and Porites astreoides, with only one 10-cm core of Acropora palmata. Most of this material is encrusted and infilled with patches of submarine Mg-calcite cement. Half of the fourth core interval (4.19-5.72 m) consists of relatively fresh Porites astreoides and is followed by a section of lightly cemented Acropora palmata with crusts of coralline algae. Another section of pavement limestone is found at the base of this interval. In the final core interval (5.72-8.21 m), the coral barrel dropped almost a meter, probably because a sand section was

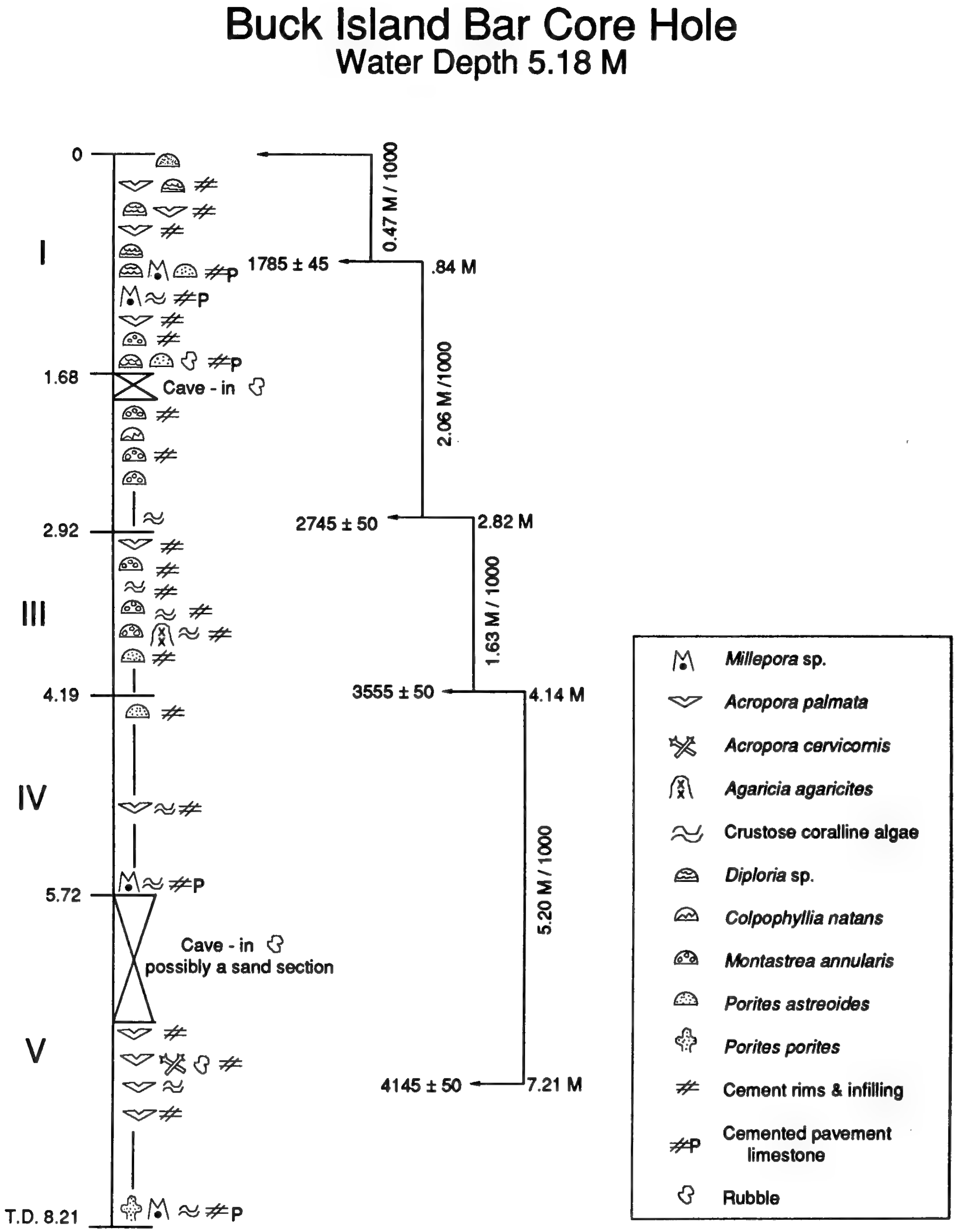

Fig. 3. Graphic summary of core data. Core intervals are indicated by roman numerals and are delineated by depths below the reef surface. Accumulation rates are recorded for intervals between radiocarbon-dated samples. Depths at right.

present. This was followed by about 1.5 m of lightly cemented A. palmata, which gives way to 8 cm of pavement limestone at the base of the core hole.

Four radiocarbon dates were obtained from four species of unaltered coral colonies--Acropora palmata, Porites astreoides, Montastrea annularis, and Diploria sp. (see Fig. 3). These dates were determined at the former Smithsonian Institution Radiation Biology Laboratory using a Libby half-life of 5,568 years and are uncorrected for $^{13}C/^{12}C$ ratios or for secular atmospheric variations.

DISCUSSION

A plot of four radiocarbon dates on a minimum sea-level curve for the western Atlantic (Lighty et al., 1982) (Fig. 4) indicates that the Holocene reef surface at the drill site has never been closer than 4.5 m to the water surface during the past 4,000 years.

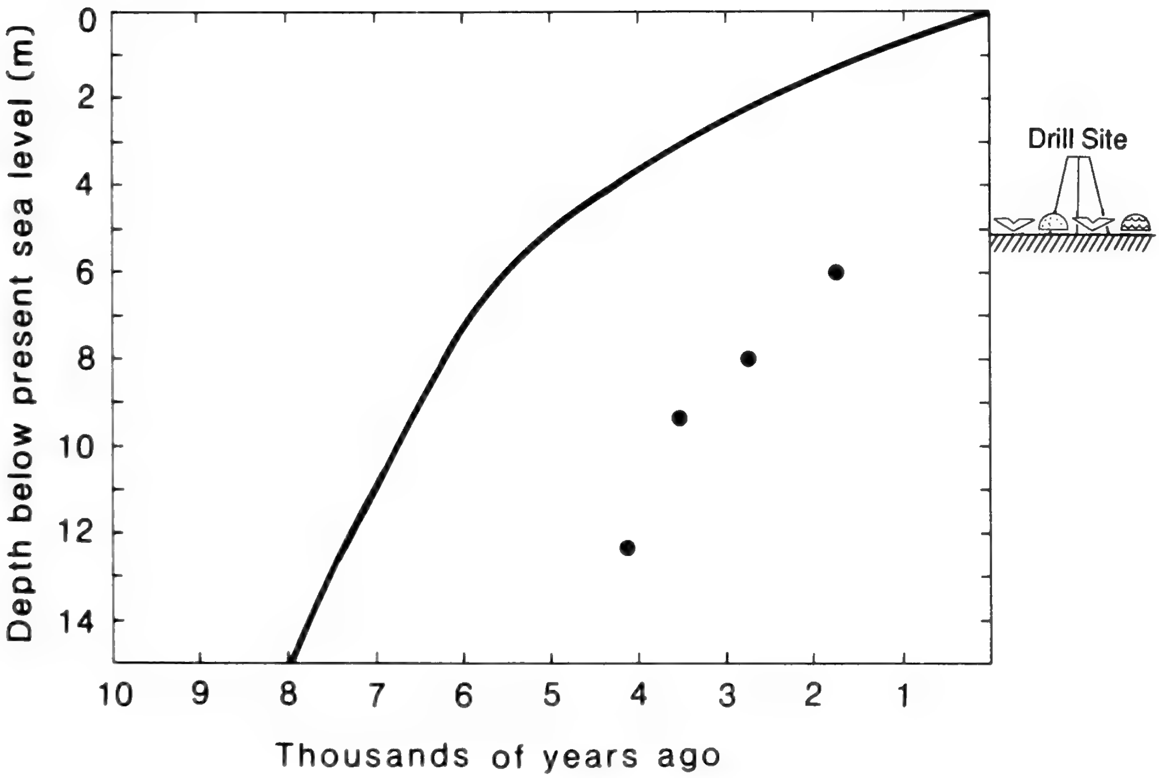

Fig. 4. Plots of four radiocarbon-dated samples on a minimum sea-level curve for the western Atlantic (Lighty et al., 1982). Present-day water depth of drill site illustrated on right side of plot.

The first three dated intervals show that the reef made some progress in catching up with the rising seas of the Holocene Transgression. The highest accumulated rate (5.2 m/1,000 years) is recorded at depths of 7.21 to 4.1 m, and probably reflects the fast growth rate of the Acropora palmata that dominates this interval (Fig. 3). The coral-head facies in the next two dated intervals only made limited progress in catching up with sea level, with accumulation rates of 1.63 and 2.06 m/1,000 years. Finally, the "race" to keep up with sea level in the last 1,785 years was lost, as is evident from the rate of 0.47 m/1,000 years estimated for the uppermost dated interval. Consequently, the present reef surface at the drill site is stranded at a depth of 5.18 m.

The sections of pavement limestone that occur throughout this core hole indicate periods in which most of the coral cover was removed--probably during storms--and the surface was left exposed for long periods of time (Macintyre and Marshall, in press). An interruption in reef growth is also reflected in the dominance of coral heads in the upper sections of the core hole. These corals (Montastrea annularis, Porites astreoides, and Diploria sp.) are all species that characteristically grow around and between stands of Acropora palmata and that are likely to remain on the substrate following the removal of this more fragile branching coral during severe storms.

The shelf edge of St. Croix frequently experiences the strong effects of extratropical winter swells--or "rollers," as they are called in this part of the Caribbean. These long-period waves can create havoc in coastal areas. Severe episodes of rollers have also been observed breaking along the entire shelf edge, even in areas where the water is 15 to 18 m deep. The devastating effects of hurricanes on reef structure, particularly the more fragile Acroporid corals has been well demonstrated in recent years (e.g., Woodley et al., 1981). Another factor contributing to the destruction of reef framework that should not be overlooked is mass mortality of corals caused by unusual temperature fluctuation or disease. In May 1989, for example, most of the thickets of Acropora palmata on Buck Island Bar were found to be dead and weakened by extensive boring by clionid sponges (M. M. Littler and D. S. Littler, pers. comm.), apparently as a result of the widespread "bleaching" that has recently attacked many corals in the Caribbean (Williams and Bunkley-Williams, 1990).

The overall pattern of reef growth on Buck Island Bar appears to be one in which Acropora palmata has thrived even at depths of 5 m--the maximum depth generally accepted for the development of A. palmata framework (Lighty et al., 1982). This coral is capable of accumulating at rates of 10 m/1,000 years or more (Adey, 1975; Macintyre and Glynn, 1976; Lighty et al., 1978). However, the deeper-water anastomosing thickets of A. palmata on Buck Island Bar are considerably more fragile than their robust shallow-water counterparts, and thus are highly susceptible to storm damage. It is not surprising that there have been frequent interruptions in the growth of this reef over the past 4,000 years--during which the branching A. palmata has been transported shoreward and the massive coral heads or bare pavements have been left

behind. The facies in the Buck Island Bar core reflects a history of catch-up/keep-up coral growth in deeper water (Neumann and Macintyre, 1985) and show no indication of a catch-up sequence in shallow water.

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CONTROL OF FERAL GOATS ON ALDABRA ATOLL

BY

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AND MARTIN B. MAIN

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CONTROL OF FERAL GOATS ON ALDABRA ATOLL

BY

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Abstract:

Recent increases in the numbers of feral goats (Capora hircus) on Aldabra Atoll, Republic of the Seychelles, raised concerns for the future of sensitive endemic biota because herbivory by goats was damaging some habitats and preventing seedling regeneration of preferred woody plants. A control program was initiated January-March 1987 in which most (n=56) of the goats on Ile Malabar were killed over 5 weeks. In addition, 292 goats were killed in the Cinq Cases region of Grande Terre over a 6-day period. A maximum kill rate of 5.15 goats/hunter-hour was achieved on Grande Terre. A second control program was conducted on Aldabra January-March 1988 and 525 goats were shot in 385 hunter-hours (1.36 goats/hunter-hour). We recommend continued efforts to eradicate the remaining goats on Aldabra.

A major threat to the biota of many insular systems is the feral goat (Capra hircus). Effects of an exotic, generalist mammalian herbivore, such as the goat, are so pervasive that Vitousek (1988) acknowledged the impossibility of preserving island ecosystems without eliminating such animals. There have been attempts to eradicate feral goats from at least 39 islands in the past 140 years (Daly and Goriup 1987); they have been eradicated from only a few (Parkes 1984, Rudge 1976, Williams and Rudge 1969). Many more islands are in need of immediate action. Information concerning the efficiency of goat control operations and their results on endemic insular biota need to be available to assist in the planning process.

Feral goats are an ecological liability on islands (Coblentz 1978, Daly and Goriup 1987, Vitousek 1988). Most reports concerning their influence on insular biota describe negative effects (reviewed by Daly and Goriup 1987, Coblentz 1978), including competition for food, removal of forest understory, severe erosion, and extinction of endemic species. Bates (1956) labelled the feral goat an "ecological dominant", and our experiences support that view. We define an ecological dominant as a species that has the ability to negatively influence structure of the physical habitat and depress production and species composition of the biota, and set back biotic succession to earlier seral stages, ultimately reducing biodiversity.

Feral goats (Capra hircus) have been present on Aldabra Atoll, Republic of the Seychelles (46°20′ E. Long., 9°24′ S. Lat., Fig. 1) in

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the western Indian Ocean, since before 1878 (Stoddart 1981); however, only recently has their presence been viewed with alarm. Goats on Aldabra (up to 17/km^2, Gould and Swingland 1980)have not achieved the high densities recorded on other, more productive oceanic islands(up to 490/km^2, Rudge and Clark 1978, 983/km^2, Williams and Rudge 1969) although Dupont (1929, cited by Stoddart 1981) reported "several thousands" in 1929.

Goat numbers on Aldabra were relatively low in recent decades (Stoddart 1971, Gould and Swingland 1980), but were believed to have increased rapidly since 1968 at which time few goats were seen or heard during a 2-month botanical expedition (F.R. Fosberg, Smithsonian Institution, pers. commun.). By 1976-77 goats were estimated at 500-600 on the atoll (Gould and Swingland 1980), and had increased to 1300 in 1985 (Burke 1988). This rapid increase prompted concern for the future of the Aldabran biota in general, and survival of the endangered Aldabran brush warbler (*Nesillas aldabranus*) in particular.

Our objective was to eradicate all goats from one of the major islands, Ile Malabar; and to assess the possibility of eradicating goats from the entire atoll.

STUDY AREA AND METHODS

Aldabra Atoll consists of 4 major islands of which 3 currently have goats (Picard, Malabar, Grande Terre). This area is a large uplifted coral atoll of 155 km^2 including mangrove areas (Gould and Swingland 1980). The climate is semi-arid (mean annual rainfall 94.1 cm, Stoddart and Mole 1977) and tropical, with a May-October dry season and a November-April wet season (Gould and Swingland 1980).

We hunted goats from 30 January to 8 March 1987 and 20 January to 15 March 1988 with centerfire (primarily .223 Rem.) bolt-action rifles equipped with telescopic (4X) sights. In 1987 all accessible areas on Ile Malabar were searched for goats and goat sign (feces, browsing, vocalizations). Goats were shot when seen, and areas having sign were hunted repeatedly until it appeared all individuals had been located and killed.

In 1987, goats were hunted for 6 days on Grande Terre. Goats killed during the first 4-day visit were weighed and examined; those killed during a subsequent 2-day visit were not. Weighing was time-consuming and was eliminated during the second hunt so that a maximum rate of kill could be determined. Our 1987 effort on Grande Terre was focused in an area about 1 km wide between the boat landing at Bras Cinq Cases and the coastal zone to the South of Cinq Cases.

During the 1988 program, most hunting effort was on Grande Terre. A 3-day visit was made to Ile Malabar to assess the success of the 1987 effort; all goats observed on Malabar in 1988 were killed. Additionally, the small population of goats on Ile Picard was hunted whenever time and weather permitted.

In both years, the number of hunter-hours of effort and the number of bullets used were recorded. Hunting in 1987 was done by a 2-person team; a 3-person team was employed in 1988.

RESULTS

Goats Killed on Ile Malabar

Fifty-six goats were killed in 1987 (Table 1), representing all goats that were observed except 2 males (that might have been killed in subsequent encounters). In 1988, the entire area hunted during 1987 was examined carefully for goats and goat sign. A single group of 5 goats was observed and killed in the Middle Camp area. There may have been other surviving goats on Ile Malabar, but we could not find them.

Of 61 goats removed from Ile Malabar during two hunts, 34 were killed in the vicinity of Middle Camp at the east end of the island, and 27 from the area adjacent to and east of Anse Malabar. In 1987 we located no sign of goats farther west than Anse Grand Grabeau, and no evidence of regular use by goats more than about 1 km west of Anse Malabar. In 1988 we encountered no goat sign west of Middle Camp.

Although we caution against excessive optimism, there are several lines of evidence that support our belief that we have nearly eradicated goats from Ile Malabar. Indeed, goats initially seen but not killed usually were observed repeatedly until killed. Nearly all goats visually identified (56 or 58) in 1987 were eventually killed. In a few areas dense vegetation made visual contact with goats difficult, although goats were often heard calling. Three groups recognizable by both adult and juvenile vocalizations were killed eventually in the general area (<1 km) where initially heard. Number and age of goats we killed invariably agreed with our expectation of group composition based on vocalizations.

Lastly, by the time we had killed what we believed to be the last goats in each area, we never again found fresh sign in that locality. For example, in the Middle Camp area where all goats killed in 1987 were shot in 5 days (Fig. 2A), no goats or fresh sign were seen in 3 subsequent days of intensive searching. In 1988 only a single group was seen in 3 days; after they were killed no other goats were evident.

Goats Killed on Grande Terre

In 1987, the first 4-day hunting effort resulted in 127 goats killed (Table 1). Because much hunting time was spent measuring and examining goats, a subsequent visit of 2 days was made to Cinq Cases to determine potential rate of kill; during this visit (1987, Cinq Cases 2, Table 1) the kill rate increased dramatically.

In 1988, we shot 525 goats (Table 1). An additional 10 goats were captured on Grande Terre and killed without shooting, for a total of 535 goats killed in 1988.

Most goats killed in 1988 (390) came from the Cinq Cases region in three hunting periods, totaling 11 hunting days, from approximately the same area that was hunted in 1987, except that hunting in 1988 extended further north past Pt. Hodoul. Only 24 of 390 goats (6%) killed at Cinq Cases were encountered and killed near the lagoon; most goats were encountered in the coastal zone.

An average of 1.36 goats killed/hunter-hour was achieved during 1988; however, this measure of efficiency varied considerably among areas hunted depending upon our level of effort and availability of goats. Efficiency in the Cinq Cases region was consistent, with 2 goats killed/hunter-hour (Table 1) during all three hunting periods. Only 0.18 and 0.31 goats were killed per hunter-hour on Ile Malabar and Ile

Picard, respectively, probably because both areas had very few goats at low density and relatively thick vegetation. Number of shots fired per goat killed varied from 1 shot/goat on Ile Malabar to 2.36 and 2.38 shots/goat at Dune D'Messe and Anse Cedres, respectively (Table 1), where goats (6 groups) were surprised at close range in thick cover.

Proportion of goats killed

Populations of feral goats tend to live in discrete ranges (Coblentz 1974). On Aldabra we were able to quickly establish the geographic limits and approximate number of individuals in relatively small populations when such populations inhabited fairly open terrain, most individuals were killed in a few days (Fig. 2).

Population sizes for Middle Camp in 1987 (N = 32) and Dune Jean-Louis in 1988 (N = 49) were estimated by the method of Leslie and Davis (1939) in which catch per unit effort (Y) is regressed against cumulative catch (x), and population size determined by the x-intercept ($N = {}^{-a}/b$). Our results indicate that we killed 91% and 90%, respectively, of the goats estimated to be present in these populations when the project began.

Large numbers of goats that inhabited the region from Pt. Hodoul to several kilometers west of Cinq Cases were a series of discrete populations. Because of time limitations we chose to work the entire area simultaneously, and as a result our kill rate remained somewhat stable throughout the entire project (Fig. 3). In this area, the estimated population (1352) was greatly in error, and if the project had continued the kill rate would have declined as goats became increasingly scarce.

In two short field seasons totaling 11 weeks on Aldabra we eliminated 883 goats. Assuming Burke's (1988) estimate (1300) was representative of the total population, we eliminated nearly 70% of the population.

Cost of eradication

Accurate calculation of the cost per goat killed during this project is tenuous. Excluding salaries, the cost per goat killed on Aldabra in 1988 was approximately $12 U.S., and about 65% of that was travel costs from Portland, Oregon, to Mahe, Republic of Seychelles. We purchased reloaded .223 caliber (soft-point) ammunition for $180 U.S./1000 rounds, therefore the bullets used to shoot goats (n = 1004, Table 1) cost $180.72 U.S., or $0.34/goat.

DISCUSSION

Consequences of goat populations on island vegetation are negative and well documented (Coblentz 1978, Daly and Goriup 1987). Taylor's (1968:62) caution that precipitous removal of goats may lead to "unexpected and even undesireable results" pales in comparison to the certain ecological catastrophe of allowing goats to remain unchecked in insular ecosystems.

Although no figure is available, there may be more than 100 islands worldwide supporting feral goat populations. Length of time goats are present on an island before being removed partly determines the recovery rate of affected plant species (Hamann 1979). For example, Hamann

reported that vegetation recovery on Isla Pinta (Galapagos), where goats existed in high nmumbers for less than 3 decades, has been considerably more rapid than on Isla Santa Fe where goats were present for at least twice as long. It can be inferred from Hamann (1979) that the sooner feral goats are eliminated from an island, the more rapidly plant species will recover because the number of viable seeds of sensitive plant species, and the number of seed producing individuals, is inversely related to the length of time that goats have been present.

Goats were severely damaging some portions of Grande Terre (Coblentz and Van Vuren 1987). We noticed extensive browsing well into the mangrove zone, and a nearly continuous browse line of roughly 2-m height on all palatable species. Regeneration of palatable woody species was nonexistent, even in areas where the endemic tortoises (Geochelone gigantea) were excluded by dense brush or jagged champignon limestone. Although tortoises are a major influence on the vegetation of Aldabra (Hnatiuk et al. 1976, Merton et al. 1976, Swingland and Coe 1979, Gould and Swingland 1980), goats are an additive influence that also can eliminate plants in refugia safe from tortoises, thus increasing the chance of extinction of sensitive species.

Results of the 1987 program on Ile Malabar were dramatically visible in 1988. Although not measured quantitatively, vegetation in the Middle Camp area was visibly more dense within 2 m of the ground and we considered this to be strong circumstantial evidence that elimination of goats allowed plants to regrow in this layer.

In former sleeping areas of goats to the east of Middle Camp, and extending to the east of Anse Malabar, areas that formerly had been browsed heavily were growing back rapidly. In these areas, Pemphis shrubs had formerly been browsed heavily as high as goats could reach. When we examined Pemphis in these areas in 1988, a luxuriant growth of basal sprouts of up to 0.5 m in length was apparent at the base of each shrub. Presumably these basal sprouts are evidence of lowered browsing pressure by goats.

Vegetation recovery on Grande Terre following the 1987 control program was not evident in 1988. We did not see regrowth of vegetation in the 2-meter-high zone browsed by goats. With the kill of an additional 390 goats in this area in 1988 we predict that growth of vegetation will proceed more rapidly.

There are two alternative levels of control for feral goats: partial reduction (control); and complete eradication. Control entails periodic efforts and prolonged expense, essentially ad infinitum. In addition, goats respond to reductions in a density-dependent manner by increasing natality (Coblentz 1982, Parkes 1984). On Raoul Island, Parkes (1984) documented an increase in productivity of goats after population reduction, whereas Rudge and Smit (1970) determined that a goat population reduced by 80% could rebound to 90% of the former level in 4 years. Consequently, control efforts must be conducted regularly to prevent rapid recovery of goat populations.

Methods other than shooting have been suggested for eradicting goats, including poisoning, introducing predators or disease, sterilizing males, and trapping. Poisoning with sodium monofluoroacetate (Compound 1080) was effective, killing >90% of goats in treatment blocks in New Zealand (Parkes 1983); however, poisoning is unacceptable for use in a World Heritage Site such as Aldabra because of

the possibility of primary and secondary effects on endemic species. Dietary overlap between goats and tortoises, and our observations of tortoises scavenging on dead goats on Grande Terre indicate the potential for nontarget poisoning, although the median lethal dose (LD_{50}) for the poikilothermic tortoises is probably high in comparison to goats (Atzert 1971).

Introduction of predators is unsuitable on Aldabra because of potential effects on endemic species. Introduction of a disease, if a suitable one could be found, might temporarily control a population, but not eradicate it. Sterilization of males is unworkable because every male would first have to be trapped or tranquilized, a prohibitively expensive and probably impossible operation. Also, killing trapped goats would be more effective than releasing them to continue damaging the environment.

If poisoning is judged unacceptable, then shooting is probably the most effective and cost efficient method of eliminating feral goats in the initial phase of an eradication program. Carefully done, large numbers of goats can be killed quickly (up to 5 goats/hunter-hour, this study), inexpensively, and humanely.

Any shooting program should minimize the number of goats that survive encounters with hunters. During the 1981-83 eradication program on Raoul Island, New Zealand, an average of 19% of goats seen escaped (Parkes 1984). During our 1987 program on Ile Malabar, 20% (14 of 70) of goats in groups that were fired upon escaped (all but 2 males subsequently killed), and on Grande Terre during the initial 4-day shooting period 11% (16 of 142) escaped (number subsequently killed unknown). During the 1988 program 14% (83 of 581) of goats in groups that were fired upon escaped, but we know that a number of these escapees were killed in subsequent encounters. Goats that escape an encounter with shooters may become more wary and difficult to kill; the last 5 goats removed from Raoul Island required a total of 2 man-years and cost $12,500 NZ each (J.P. Parkes, New Zealand Forest Service, 1985 personal communication to D.W. Baber).

We believe that the 3-person shooting team employed in 1988 was a trade-off between increased firepower and increased risk of alarming goats. Escape by goats that were fired upon was not substanitally affected by the additional firepower, nor was the number of bullets fired per goat killed. We did notice in several instances that there was insufficient cover to conceal 3 stalking hunters, and in such instances goats became alarmed sooner than if there had been two hunters. The highest kill rates (5 goats/hunter-hour) and lowest expenditure of ammunition per goat killed (1.4 bullets/goat, Ile Malabar, 1987) were accomplished by the 2-person team.

Differences in rate of kill and accuracy among areas hunted (Table 1) resulted from several factors including group size of goats, amount of cover available for stalking, distance to goats when first observed, and level of excitability of goats that were encountered. In contrast, the stable rate of kill achieved during three hunting periods at Cinq Cases in 1988 (Table 1) was due to the combination of a large population in a large area, limitations on how much area could be covered in a day, and to our improving ability to anticipate, find, and shoot goats even as populations declined.

We expected that difficult terrain (champignon limestone), dense vegetation and extreme heat would combine to make the eradication of goats on Aldabra difficult, but control was easier than anticipated. We attribute this to our experience from similar projects, and the relatively narrow landmass forming the ring of the atoll. We believe that goats can successfully eradicated from Aldabra. We have demonstrated that large numbers can initially be killed; after the majority have been killed, as they were by our efforts, the remainder can be efficiently located and killed through the use of radiocollared "Judas goats" (Taylor and Katahira 1988). In this technique the gregarious sociality of the goat is exploited by repeatedly relocating radiocollared goats and shooting the other members of their groups. Judas goats repeatedly (Taylor and Katahira 1988) and quickly (BEC, pers. obs., San Clemente Island, California) locate other goats.

SUMMARY

Recent increases in the numbers of feral goats on Aldabra Atoll, Republic of the Seychelles, raised concerns for the future of sensitive endemic biota because grazing by goats was damaging some habitats and preventing seedling regeneration of preferred woody plants. We initiated a control program, by shooting, in January-March 1987 and continued January-March 1988. In 11 weeks on Aldabra, 883 goats were eliminated, including most ($\underline{N}$ = 61) inhabiting Ile Malabar. In small populations living on relatively open habitats, most individuals (91% Middle Camp, 90% Dune Jean-Louis) were killed in only 5 days of hunting. Our total kill may have been as high as 70% of the goat population on Aldabra.

Goats shot/hunter-hour ranged from a low of 0.18 (Ile Malabar, 1988) to 5.15 (Cinq Cases 2, 1987). The mean efficiency was 1.36 goats shot/hunter-hour in 1987 and 1.61 in 1988. The cost per goat killed in 1988 was approximately $12 U.S.; ammunition costs were only $0.34 U.S. Most of the costs were for transportation.

We demonstrated that large numbers of goats can be killed quickly and cheaply on Aldabra, and probably many other islands as well. Because of numerous direct and indirect effects of goats on insular biota, we strongly advocate removal of the remaining goats from Aldabra in particular, and from sensitive oceanic islands in general. We recommend that goats be killed by shooting them with small caliber centerfire rifles by trained 2-person teams of marksman.

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Table 1. Numbers of goats killed, hunter-hours, number of shots fired, and efficiency of hunting by location for goats killed on Aldabra Atoll, Republic of the Seychelles, January - March 1987 and January-March 1988.

Location	Goats Shot	Hunter-Hours	Shots Fired	Goats Shot/ Hunter-Hour	Shots Fired/ Goat Killed
1987					
Ile Malabar	56	127.5	77	0.44	1.38
Cinq Cases - 1	127	56	217	2.27	1.71
Cinq Cases - 2	165	32	--[a]	5.15	--[a]
Total 1987		348	215.5	--	1.61
--					
1988					
Cinq Cases - 1	130	66	218	1.97	1.68
Cinq Cases - 2	164	76.5	332	2.14	2.02
Cinq Cases - 3	92	48	175	1.92	1.90
Dune Jean-Louis	42	40.5	73	1.04	1.74
Dune D'Messe	14	29.2	33	0.48	2.36
Dune Blanc-Gros Ilot	62	66	136	0.94	2.19
Anse Cedres	8	4.5	19	0.56	2.38
Ile Malabar	5	28.5	5	0.18	1.00
Ile Picard	8	26	13	0.31	1.62
Total 1988	525	385.2	1004	1.36	1.91

[a] data not gathered during this hunt

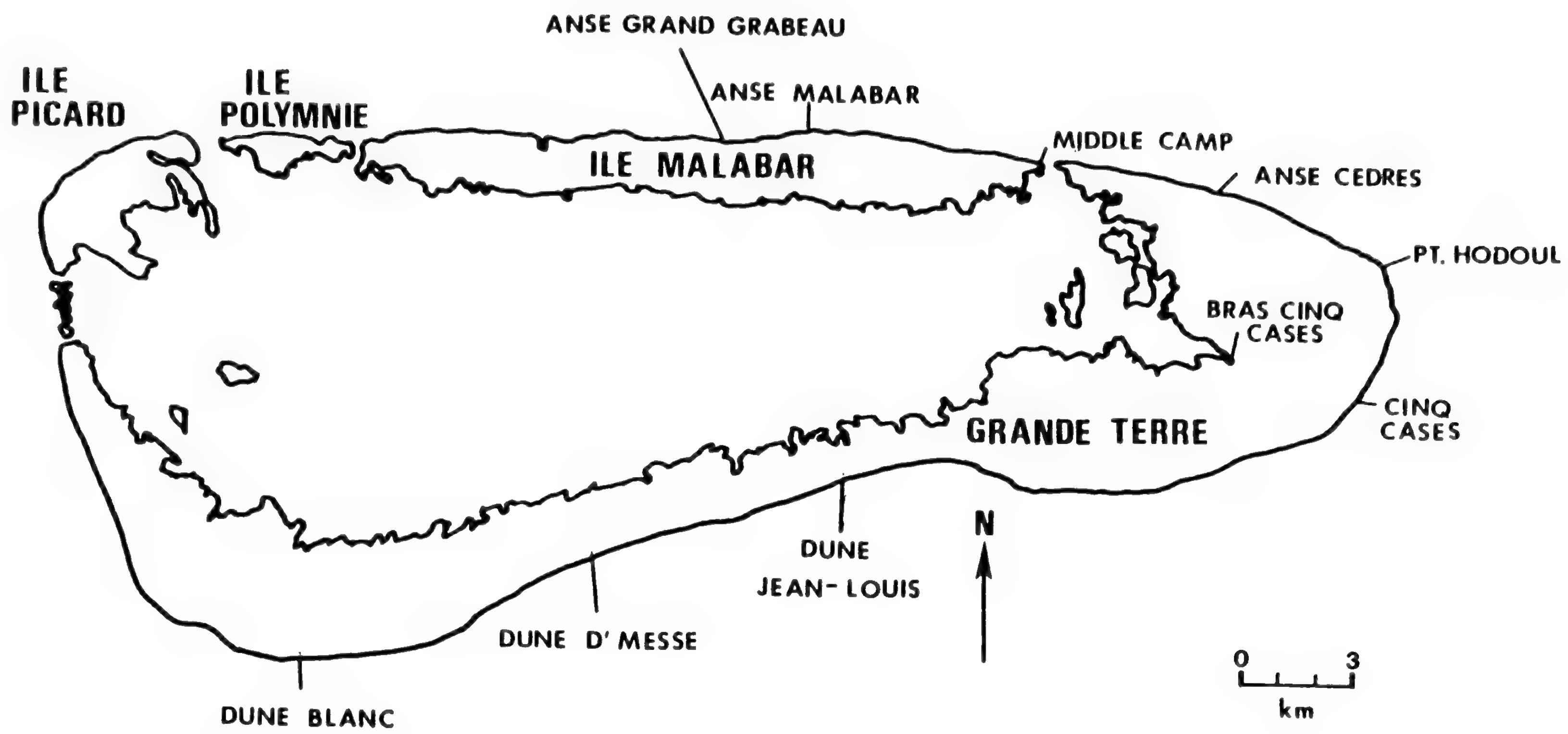

Figure 1. Aldabra Atoll, Republic of the Seychelles, showing placenames in areas where goats were hunted.

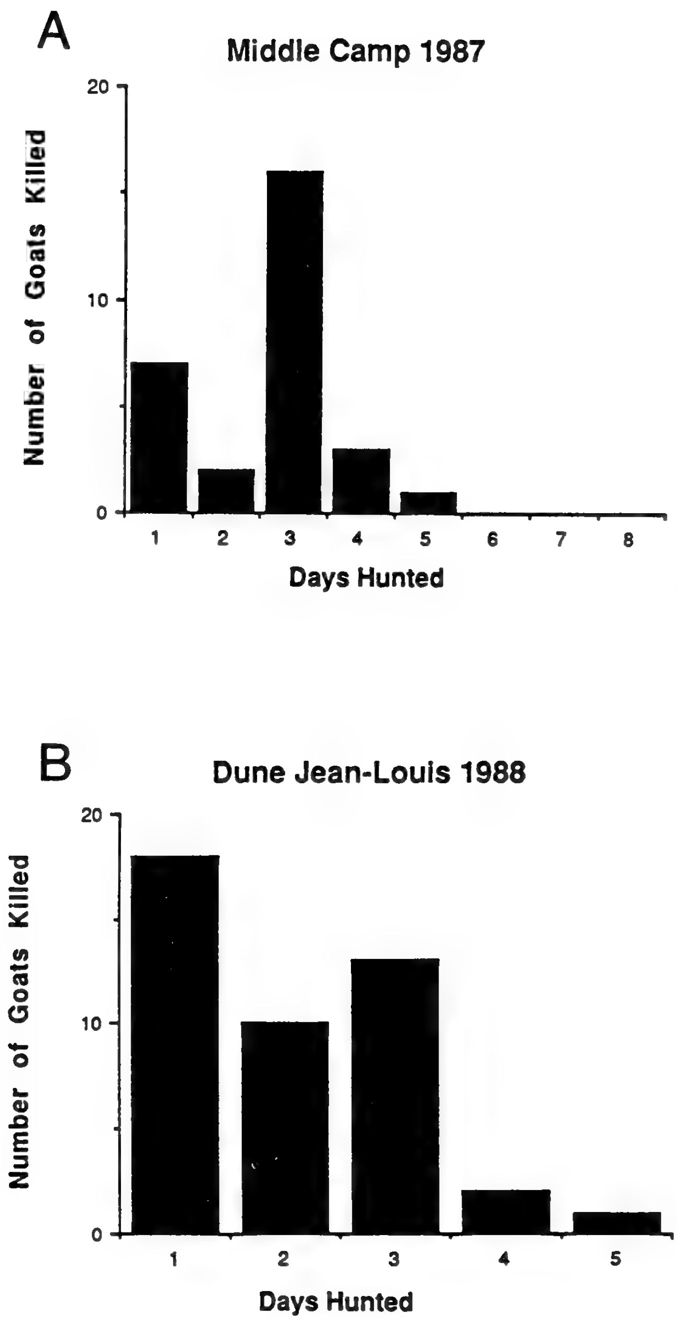

Figure 2. Number of goats killed on successive days of hunting at Middle Camp (A), and Dune Jean-Louis (B), Aldabra Atoll, February, 1987 and January, 1988, respectively.

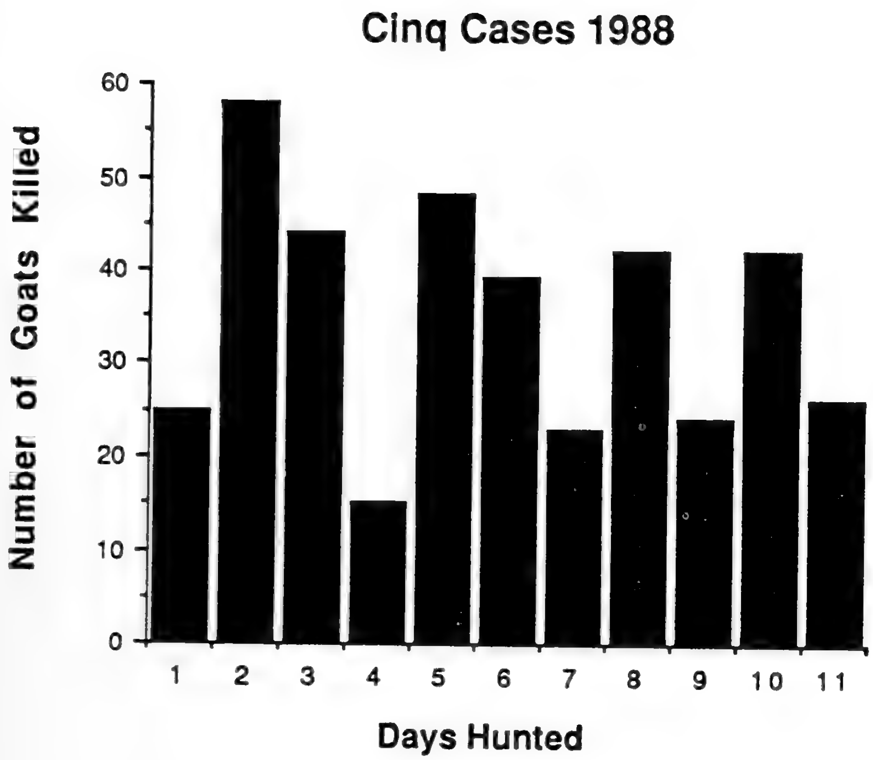

Figure 3. Number of goats killed on successive days of hunting in the Cinq Cases - Pt. Hodoul region, Aldabra Atoll, January-March, 1988.

ATOLL RESEARCH BULLETIN

NO. 338

FERAL CAT ERADICATION ON A BARRIER REEF ISLAND, AUSTRALIA

BY

STEVEN DOMM AND JOHN MESSERSMITH

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BY

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INTRODUCTION

North West Island (23 42'S, 151 17'E) is a densely vegetated sand cay located 30 nautical miles northeast from Cape Capricorn in central Queensland. At 105 ha this is the largest island in the Capricornia Section
Great Barrier Reef Marine Park and the most important nesting site for the wedge-tailed shearwater (Puffinus pacificus) on the Barrier Reef. Feral cats (Felix catus) on the island probably originated from domestic cats that escaped during either guano mining in the late 1800s or during a turtle soup processing operation in the early 1900s.

Shearwaters are present on the island for approximately six months of the years from October to about April, nesting in burrows dug in the sand and have no defense against cats. With an estimated population of 724,560 shearwaters (Hulsman, 1984) visiting North West Island each year a large number were killed by feral cats. Evidence of this predation was obvious in the abundance of dead shearwaters found throughout the island.

The feral cat occurs over much of mainland Australia where it preys upon the native fauna, in some cases seriously reducing native animals. On islands however, it has played a major role in the eradication of native birds. In New Zealand alone, these predators are implicated in the extinction of at least 6 endemic species and over 70 localized subspecies (Rauzon, 1985). The Queensland National Parks and Wildlife Service has a policy aimed towards the eradication or control of feral animals on national parks. In keeping with this policy and because a high level of predation by a feral animal on nesting sea birds was not acceptable, it was decided to eradicate the feral cats on North West Island.

METHOD

Three eradication methods were used:

. shooting (12 gauge shotgun)
. trapping (wire cage traps)
. poisoning (1080 poison on fish bait)

Trapping was undertaken using wire cage traps (600 mm x 600 mm x 400 mm) using a variety of baits including fish, cat food, and tinned tuna. The traps were placed in locations known to be visited by cats. After approximately 40 trap nights this technique was abandoned. Shooting between February 1984 and February 1985 consisted of six separate trips averaging four days per trip with one or two people. Shotguns used were a double-barrel and pump-action 12 gauge with No. 3 duckshot. The cats were hunted throughout the day over the whole island by either walking marked transects or by random searching. Spotlight shooting at night along the beach was also used. When the number of cats diminished to the stage where shooting was no longer time efficient the poisoning program commenced.

The poison used was 1080 (Sodium monofluroacetate) which is tasteless, odorless, and colourless. It is also readily biodegradable in soil, easy to handle, and more humane than alternatives (Allen 1983). Non-target fauna does not occur on the island therefore the program could proceed without constraint. Winter was chosen as the time for baiting as food is scarce for feral cats due to the absence of shearwaters and reduced numbers of other sea birds. Fifty kilograms of shark flesh was cut into 5 cm cubes and each injected with approximately 2 mls of a 0.6% 1080 solution (the same concentration is used on feral dogs). As the baits were injected, the 1080 solution would normally flow out over the surface of the bait. Smaller and thinner pieces of shark flesh were sprayed with 1080 solution and placed in heavy duty plastic bags along with large injected baits. The baits were then placed in styrofoam eskies and frozen prior to transport to North West Island. Baits were placed over the entire island in a 60 m square grid. Extra baits were placed where cats are known to forage at night. Baiting was first carried out in August 1985 and repeated using the same method September 1985. A random sample of cats shot was weighed, total length measured (head, body, tail), and the stomachs of 19 cats were removed for subsequent stomach analysis.

RESULTS

The total of cats confirmed killed were 105, comprising:

- 8 trapped
- 95 shot (16 at night)
- 2 dead cats seen after baiting

Of the adult cats killed, 57.5% were males and 42.5% female. Two adult males and three adult females were trapped, and 44 adult males and 31 adult females were shot. Trapping resulted in three juvenile (unsexed) cats being caught while shooting accounted for 20 juveniles.

Trapping was found to be ineffective early in the eradication program and was abandoned in favour of shooting. Shooting was most effective in the forest during the day provided the shooter moved slowly and quietly. The cats were active throughout the day but appeared to hunt only a night. Spotlight shooting accounted for 16.8% of the cats shot, but was not considered as effective as daytime shooting.

An unknown number of cats is suspected of having died undetected following poisoning. Animals poisoned with 1080 are seldom found near the baiting site because of the time lag (up to 2 hours with dogs) before death occurs with this slow acting poison (Allen 1983). Two dead cats were found by chance after the first baiting program.

All cats were of a tabby colour (mottled dark brown and grey) with an average adult weight of 3.16 kg and an average length of 749 mm taken from front of head to end of tail. Stomach contents of 19 cats were examined. Most contained seabird remains, insect such as cockroach and centipede, the remains of what might have been a mouse, or were empty. All cats killed appeared in good physical condition.

In November 1986 a detailed survey of North West Island revealed no feral cats. The beaches were checked for tracks and the interior of the island checked for cats or dead birds which in the past were numerous. No substantiated reports of cats were received from campers on the island between October 1985 and November 1986.

DISCUSSION

A recent report on feral cats on Jarvis Island, (Rauzon, 1985) an atoll located 1300 nautical miles south of Hawaii, gives comparable data to that of North West Island as both are relatively small islands located in the tropics. The shooting success on North West compares favourably with that of Jarvis: the success rate of North West was approximately 0.5 cats per hour over the entire hunting period; that of Jarvis was initially 1.97 but dropped off to 0.19 cats per hour. The sex ratios of cats appear roughly similar for both islands with those from Jarvis Island being 52% female and 48% male (North West totals were 57% male, 42% female for shooting). The differences could be due to small sample sizes. Poisoning was also used on Jarvis Island the results of which were uncertain.

Jones and Horton, 1984 in a study of gene frequencies and body weights of feral cats from six localities including Macquarie Island record the mean weight of males and females studied at 3.82 kg. This is heavier than 3.16 kgs recorded from North West Island. This could be explained as a seasonal fluxuation in body weight reflecting food availability or perhaps over many generations of cats on North West became lighter in weight because of some genetic advantage. Except for a short while after heavy rain there is no reliable source of fresh water on North West Island. Evidently this shortage is not critical to feral cats survival, however it might account for the lighter body weight which may be an island adaptation.

Camper complaints indicate the population of mice on North West Island are increasing since eradication of the cats. This was expected. The numbers of mice can be controlled by long term baiting.

The eradication of feral cats from national parks can be difficult, expensive, or impossible. The experience on North West Island indicates that in some situations eradication of feral cats on a low cost basis is possible. This was the result of several factors:

- small size and flat topography of North West Island
- a lowered vigilance by the cats resulting from a long history with no natural predators and abundant food
- type of forest lacking a grassy understory resulting in good visibility for hunting
- absence of non-target species susceptible to the poison
- easy accessibility to the island by national parks staff

With the eradication of feral cats on North West Island the buff-banded rail (Rallus philippensis) should return. This bird which is common on all the islands in the Capricornia Section Marine Park is absent on North West Island due to past predation by cats. Ground nesting terns which also nest on the other nearby islands may commence nesting on North West Island following the removal of cats. Regular patrols by Queensland National Parks and Wildlife Service ranger staff will monitor any changes that occur to the island fauna.

ACKNOWLEDGEMENTS

I would like to thank the Rockhampton based Queensland National Parks and Wildlife Service staff who helped us in the project both in the field and by commenting on the manuscript.

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BOOK REVIEW

Marine Plants of the Caribbean. A Field Guide from Florida to Brazil. By D. S. Littler, M. M. Littler, K. E. Bucher, and J. N. Norris. Smithsonian Institution Press, Washington, D.C. 20560, USA. 221 color, 7 B & W illus. 5 x 7 5/8, 272 pp. 1989. Price: US$14.95

This colorful little book is the type of field guide that is desperately needed by all those who are interested in observing or studying the great diversity of plants and animals that inhabit the shallow tropical seas, particularly around coral reefs.

In organizing this book, the authors have kept the nonspecialist in mind and have avoided complex scientific terminology and taxonomic keys. The algae are grouped by color and indexed by color-coded pages, then further subdivided on the basis of their growth patterns.

Most of the book is devoted to the identification of marine algae, but it also includes two pages on the microscopic diatoms and dinoflagellates in addition to an introduction to five seagrasses, the flowering plants of the sea. The reader is provided with excellent color photographs of each plant and a brief description of its basic characteristics and habitat preferences--in much the same format as that used in the popular bird and insect guidebooks.

The authors are to be commended for their clear introduction to the classification, growth forms, and scientific names of marine plants. They also describe the reef and mangrove areas that these plants inhabit and give helpful hints on how to collect and photograph them. The water-resistant cover is an additional bonus that makes this a truly usable field guide for both scientists and tourists.

One word of caution: As the authors point out, this book covers the more abundant Caribbean marine plants, which account for only about one-third of the known species of this area. Users must therefore avoid making hasty identifications when they find a species that seems to resemble one in the book. These plants are not always easy to distinguish. For example, <u>Rhipocephalus</u> <u>oblongus</u>, which is not covered in the book, might be confused with <u>Penicillus</u> <u>capitatus</u>, both of which have similar growth patterns.

This publication can be ordered from Smithsonian Institution Press, Department 900, Blue Ridge Summit, PA 17294, USA. An additional $2.24 should be included for postage and handling costs.

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Articles submitted for publication in the Atoll Research Bulletin should be original papers in a format similar to that found in recent issues of the Bulletin. First drafts of manuscripts should be typewritten double spaced. After the manuscript has been reviewed and accepted, the author will be provided with a page format with which to prepare a single-spaced camera-ready copy of the manuscript.

ATOLL RESEARCH BULLETIN

NO. 339

PACIFIC ATOLL SOILS:
CHEMISTRY, MINERALOGY AND CLASSIFICATION

BY

R. J. MORRISON

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BY

R. J. MORRISON

Atolls are essentially reefs of variable thickness built up by corals (and other organisms) resting on a volcanic base; they are unique to tropical and certain subtropical oceans since the reef-building organisms require water temperatures in excess of 22°C. Atolls are widespread in the South Pacific occurring from Oeno and Ducie east of French Polynesia to Papua New Guinea in the west, from the Northern Marshall Islands in the north to New Caledonia in the south. Some countries consist entirely of atolls e.g. Kiribati, Tuvalu, Tokelau, others contain atoll groups e.g. the Tuamotu Archipelago in French Polynesia; and some countries consist of mainly volcanic islands with a few isolated atolls e.g. Ontong Java in the Solomon Islands.

The classical form of an atoll is a more or less continuous emerged or slightly emerged calcareous reef surrounding a lagoon but Cumberland (1956) has identified six types of island in the Pacific partly or wholly associated with coral reefs. In this paper we shall consider atolls as being of two major types;
(a) low atolls where the maximum height of the emerged portion (usually less than 5 m) is made up of accumulations of broken reef material deposited by storms, e.g. Takapoto in French Polynesia, Tarawa in Kiribati, and
(b) raised atolls where the whole island has been tectonically uplifted and the atoll morphology largely

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fossilized (new fringing reefs may have developed around them) e.g. Lifou in the Loyalty Islands (New Caledonia), Nauru and Niue. This latter group is also often referred to geologically as raised coral platforms.

The deposition and accumulation of volcanic ash and/or pumice has occurred on many atolls, but the extent of this occurrence decreases on moving from the tectonically active zone of recent volcanism (10-25°S) in the south-west Pacific towards the equator.

The widely varied nature of atolls makes it difficult to generalise about them but many have some features in common. They usually have limited land area and few natural resources. Low atolls, particularly in the eastern Pacific have limited supplies of fresh water and many are subject to prolonged droughts. The groundwater is often brackish (slightly salty). This peculiar environment has resulted in the development of a specialised flora - a plant community adapted to saline, alkaline soils, subject to water stress and salt spray. The natural vegetation is mostly strand species recruited from the Indo-Pacific strand flora of the shores of islands of all kinds in the region. The agriculture is also rather specialised, often being restricted to coconuts, pandanus, breadfruit and such root crops as Colocasia and Cyrtosperma grown in pits dug down to the groundwater table.

The raised atolls frequently have significantly greater land areas and usually have received additions of volcanic or other non-calcareous materials. The greater land area usually has a larger associated groundwater lens that can be exploited for human consumption or irrigation but the rainfall is still generally related to location and in the central and eastern Pacific prolonged droughts are common. On the raised atolls the soils are usually older and better developed as is the native vegetation. Substantial forests of Calophyllum and related species have developed on many of these raised islands.

A more detailed discussion of the chemistry and mineralogy of the soils from a number of islands is included later in this paper, but some general points about atoll soils can be made at this point. Soil properties are to a large extent dominated by the calcareous nature of the parent material, whether or not this is covered with volcanic ash or other materials. The soils tend to be shallow, alkaline, coarse textured, having carbonatic or (where non-calcareous deposits have accumulated and weathered e.g. Lifou, Niue) oxidic mineralogy except where there have been relatively recent

additions of volcanic ash. The soils are generally of very low silica content. The fertility is highly dependent on the organic matter content. Organic matter can be high in undisturbed soils under natural vegetation, but can decrease dramatically as a result of inappropriate cultivation techniques e.g. land clearance and weed control by fire.

As for all tropical soils, organic matter in atoll soils performs an important role in the concentration and cycling of plant nutrients. In atoll soils, however, a second role - that of moisture retention - is equally important. Since atoll soils are frequently sandy and excessively well drained, the moisture retention in the absence of organic matter is very low; the total amount of water retained often remains low and plants are subject to water stress unless the rainfall is high and relatively constant or they can tap the freshwater lens.

Guano deposition is common on atolls, giving reasonable supplies of phosphorus. Potassium levels, on the other hand, are frequently extremely low, and the neutral to alkaline pH of these soils can make several of the trace elements, particularly iron, manganese and zinc, unavailable to plants. The coarse texture, high pH and calcium domination of the exchange complex of many atoll soils would tend to indicate a low capacity to retain sulphur, but some sulphur is made available continuously by solution of the coralline materials which typically contain 0.2-0.3% sulphur plus atmospheric sulphur derived from sea-spray.

For the purposes of this discussion, atoll soils will be considered in 2 groups - low atolls and raised atolls. For the low atolls information from Tarawa, Tuvalu, Cook Islands and the French Polynesian atolls of Takapoto and Tikehau will be considered, while discussion of raised atolls will be restricted to Lifou in New Caledonia, Nauru and Niue.

CHEMISTRY OF LOW ATOLL SOILS

Tarawa in Kiribati (173°E, 1°20'N) is a typical example of a low atoll. It is roughly triangular in shape with the southern arm being one of the most densely populated areas in the Pacific islands. Recently the soils of two areas have been studied in detail (Seru and Morrison, 1985; Morrison and Seru, 1986). The chemical data obtained are typical of those for soils of low atolls.

Many of the properties are related to the organic

matter content of the topsoil. Organic carbon values vary from about 2-20% depending on the age of the soil, the vegetation and soil management. In the subsoils organic carbon values are always low (<0.5%) unless there has been considerable soil disturbance,e.g., due to the digging of <u>Cyrtosperma</u> pits. Nitrogen values follow the organic contents closely as C:N ratios usually range from 9-12 for topsoils and 8-12 for subsoils. Water retention against 15 bar pressure is closely correlated with organic matter content; values of 5-25% have been obtained for topsoils, while for subsoils the values are always low (2-4%). Cation exchange capacity is also closely related to organic matter for topsoils with values in the range 6-60 cmol/kg while the values for the sandy calcareous subsoils are usually less than 2 cmol/kg. Exchangeable magnesium values are generally around 4-6 cmol/kg, sodium contents are about 0.2 cmol/kg but potassium values are always low rising about 0.1 cmol/kg only in topsoils with substantial organic matter contents.

The calcium carbonate content is always high ranging from 55-90% for topsoils and being greater than 90% for subsoils. This dominance of the enviroment by carbonate leads to high pH values; pH (water) values for topsoils were in the range 7.5-8.5 and for subsoils 8.5-9.1; pH ($CaCl_2$, 0.01 mol/L) values were in the range 7.1-7.6 for topsoils and 7.5-8.0 for subsoils.

Extractable phosphorus (Olsen procedure) values are generally low (5-15 mg/kg) for topsoils and very low (<1 mg/kg) for subsoils. The total phosphorus contents vary considerably ranging from 500-30,000 mg/kg for topsoils and from 300-5000 mg/kg for subsoils. Phosphate extractable sulphate values range from 20-50 mg/kg for topsoils but are generally low (<20 mg/kg) in subsoils. Total sulphur values are fairly constant at around 4000 mg/kg for all soils.

Tuvalu consists of 9 islands lying between 5° and 10° S latitude and 175° and 180° E longtitude. The islands are all low atolls, free of any major deposits of volcanic materials although phosphatic materials are concentrated in small areas. As part of a programme to develop some intensified agriculture (S.Caiger, personal communication) a number of soil samples have been analysed at the Land Resources Development Centre Laboratory (UK) and at the University of the South Pacific Institute of Natural Resources Laboratory in Suva. Examination of these data (Table 1) shows that there are many similarities with that obtained on Tarawa. One major difference is the presence in Tuvalu of areas of known phosphate accumulation. These may be related to bird nesting activities associated with

TABLE 1. Chemical Data for Some Tuvalu Soils

Determination		TOPSOILS Range	SUBSOILS Range
pH 1:5 H_2O		7.4-8.6	8.1-9.1
E.C. ms/cm 1:5 H_2O		0.13-0.45	0.10-0.21
$CaCO_3$ %		42-96	80-966
Exchangeable	Na	0.1-0.9	0.2-0.3
Cations	K	0.0-0.2	0.0-0.2
(cmol/kg)	Mg	2.1-7.6	3.8-5.9
CEC (cmol/kg)		3.7-27.1	1.8-4.2
Total N %		0.2-0.65	0.05-0.13
Org C %		1.97-14.66	0.3-1.12
Olsen P ppm		9-480	4-560
Total	P	560-58500	845-54500
(mg/kg)	K	100-400	100-200
	Mn	15-60	20-100
	Cu	25-90	45-95
	Fe	10-400	10-500
	Zn	10-250	10-280
Hot H_2O sol B ppm		0.3-1.9	0.3-0.4

specific vegetation types in the past. These areas give very high total phosphorus values (2-5% P) and high Olsen extractable phosphorus values (> 50 mg/kg).

The data here also clearly indicate the very low levels of certain micronutrients found in the soils of low atolls. Iron, manganese, copper and zinc are all present in extremely low (total) amounts, such that the plant available supplies of these elements must be minimal in the absence of external supplies.

Data obtained for the soils of Manuae and Palmerston in the Cook Islands (Bruce, 1972) show very similar patterns to those described above. pH values from 7.1-8.3, organic carbon contents of 2-6%, C/N ratios of 11-18, total phosphorus levels of 100-1600 mg/kg and available phosphorus of 20-80 mg/kg were recorded. CEC values were generally low (5-26 cmol/kg) with very low levels of potassium.

Tercinier (1969) in his discussion of Takapoto also stresses the importance of the organic matter content. He observed a relationship between organic matter and water retention. Organic matter increases in moving from the ocean sides, bombarded by waves to more stable areas near the lagoon. The cation retention capacity of the soils is also closely related to the organic matter content and the accumulation of nitrogen, phosphorus and potassium in the organic rich surface layers was observed.

On Tikehau, Jamet (1985) found that the calcium carbonate content of topsoils was 80-90% with generally more than 90% in the subsoils. Total potassium content was always low (<0.05%) as was exchangeable potassium (<0.3 cmol(p+)/kg) while the phosphorus levels varied depending on whether or not significant guano deposition had occurred. Subsoil pH values usually were between 8 and 9, but in the topsoils with relatively high organic matter contents the values ranged from 7.0-7.5.

Thus it can be seen that in the low atolls the soils are alkaline, with most of the soil "fertility" related to the accumulated organic material. Under these conditions nitrification is favoured but toxic accumulations of nitrate are unlikely unless there are unusual hydrological conditions. Volatilization of nitrogen as NH_3 from ammonium and urea fertilizers will occur, with particularly large losses occuring if these materials are not incorporated. The availability of phosphorus is controlled by calcium activity and much fertilizer P will be precipitated as calcium phosphates or adsorbed on the surfaces of the carbonates. Band applications of P are

recommended so that P will be available to seedlings soon after emergence. K availability is decreased by high Ca and/or Mg levels; the low levels of K in the coral limestone parent materials mean that this element will always be in short supply.

Supplies of available Ca and Mg are plentiful in low atoll soils but imbalances with K and micronutrients cause significant plant nutrition problems. Sulphur is usually available in small quantities from solution of limestone and from rainwater but if crops with large S requirements are grown intensively, external additions will be required. Available B decreases moderately with increasing soil pH, but few B deficiencies have been reported on calcareous soils. Mo solubility and availability increase with increasing pH but low Mo contents in the parent rock may lead to deficiencies.

Solubilities of Cu, Fe, Mn, Zn decrease with increasing soil pH. Cu deficiencies are less related to soil pH than are those of the other micronutrients. Zn forms relatively insoluble zincates in calcareous soils and Fe uptake is reduced by high bicarbonate concentrations in the soil solution. With the relatively low contents in coral limestone all of these elements are likely to be highly deficient in soils of the low atolls.

MINERALOGY OF LOW ATOLL SOILS

As the soils of the low atolls are dominated by calcium carbonate the mineralogy is almost exclusively carbonate. The dominant minerals are calcite and aragonite, the common forms of calcium carbonate deposited by reef forming and reef living organisms. Calcite contains varying amounts of magnesium (substituting for calcium in the mineral structure). If the magnesium content is >1%, the mineral is described as high magnesium calcite; other forms are referred to as low magnesium calcite. There is considerable variation in the mineral content of low atoll soils as illustrated below.

The results of the mineralogical analyses of samples from several pedons on Abatao Islet, Tarawa are summarised in Table 2 (Morrison and Seru, 1986). These confirm the dominance of the 2 principal forms of calcium carbonate-calcite and aragonite. In contrast to the lagoon sediment mineral samples, (Weber and Woodhead, 1972) calcite is the dominant mineral in all of the soil samples with aragonite being the minor component. The relative proportion of high and low magnesium calcite varies but there is no particular pattern to this variation except that high magnesium calcite tends to dominate in soils on the lagoon

TABLE 2. ABATAO SOILS : APPROXIMATE MINERALOGICAL COMPOSITION (< 200 MESH SAMPLES)

SOIL	DEPTH (cm)	ARAGONITE	CALCITE (High Mg)	CALCITE (Low Mg)	OTHERS
TRW 7	6 - 31	3	5 (> 70%)	2	
8	31 - 60	2	5 (> 70%)	2	
9	0 - 15	3	4	3	Apatite 2
9	50 - 60	2	5 (> 70%)	2	
10	45 - 55	2	5 (> 70%)	1	
11	40 - 50	3	5 (> 70%)	1	
12	0 - 18	3	2	5	
13	0 - 25	2	2	5 (> 70%)	
16	0 - 6	2	4	5	
17	0 - 11	3	5	3	
17	40 - 55	3	5 (> 70%)	2	
18	0 - 13	2	4	5	

5	> 50%
4	30 - 50
3	15 - 30
2	5 - 15
1	< 5%

side of the islets. Apatite was detected in only one sample.

The mineralogy data for the Tarawa soils are in general agreement with the observations of Hathaway (1965) for soils of the Northern Marshall Islands. Hathaway found that high magnesium calcite was the dominant mineral in most soils, except for the coarsest fragments is some profiles where aragonite was the major constituent. Low magnesium calcite was present in only one sample. Hammond (1969) in a study of soils of Christmas Island (Kiritimati) found that aragonite was the dominant component, this mineral being present in the greatest amounts in the coarse fragments. Calcite was more abundant where foraminifera dominated the deposits. Most calcite was high in magnesium but low magnesium calcite was present mainly in the coarse sand, very fine sand and silt fractions.

Samples from Manuae and Palmerston showed a general dominance of aragonite over calcite with the aragonite content being greatest in the coarser soils (Bruce, 1972). Significant amounts (10-20%) of apatite were also detected and a small amount of an unknown amorphous material was present in all samples.

Aragonite which forms the hard parts of corals or algae and high magnesium calcite from algal skeletal material are more abundant in most shallow water marine environments than low magnesium calcite, but among deep sea oozes rich in calcitic foraminifera and coccoliths, the more stable low magnesium calcite is the predominant phase (Chave, 1962). It should be noted that low magnesium calcite is the thermodynamically stable phase under the conditions prevailing at the Earth's surface.

The presence of substantial quantities of low magnesium calcite in the surface horizons of four Abatao pedons is of considerable interest. While this mineral was found on Christmas Island it was always a minor component (Hammond, 1969) and was only detected in one Northern Marshalls sample (Hathaway, 1965). The presence of this mineral may be caused by surface addition of algal skeletal material of low magnesium content or may be the result of alteration of aragonite to calcite, although the latter process was considered to be of little importance in the Northern Marshalls (Hathaway, 1965). Chave (1962) in a study of carbonate sediments found an increase in low magnesium calcite content with decrease in particle size and ascribed this to a selective loss of unstable minerals due to inversion (to a more stable form) or solution.

CLASSIFICATION OF LOW ATOLL SOILS

One of the major difficulties encountered when considering the classification of atoll soils is the major change that has taken place in soil classification over the last 50 years. Much of the early work on atoll soils was carried out by American scientists working in the central and western Pacific Islands in the 1940's and early 1950's. At that time soil classification was based on the system developed for publication in the 1938 "Soils and Men" monograph (Baldwin et al., 1938). As pointed out by Smith (1983) this system of classification was produced hurriedly to meet the publication deadline and as a consequence many facets were incompletely developed and defined. Although the '1938' system underwent a series of modifications up until 1959, it was recognized by 1950 that major difficulties could not be overcome and that the development of a new system was essential if a satisfactory taxonomy was to be obtained. The new taxonomy was developed through a series of approximations and published in 1975 as Soil Taxonomy (Soil Survey Staff, 1975). Soil Taxonomy is now widely used throughout the world and is continually being modified as new information or better criteria for grouping soils become available. In this paper all soils are classified according to Soil Taxonomy but, where appropriate, relationships to the '1938' system (and its modifications) are included. Prior to discussing the details of the classification of individual soils, some introductory comments on the two systems are presented.

In the '1938' system (particularly after the revisions up to and including 1949) soils were classified in a hierarcheal system having six categories - order, suborder, great soil group, family, series and type. Three soil orders (Zonal, Intrazonal and Azonal) were developed. Atoll soils were included in the Halomorphic and Calcimorphic suborders of the Intrazonal soils plus the Azonal soils (no suborders were prepared for this order). The principal great groups were Rendzina soils, Lithosols and Regosols. Rendzinas were soils having dark coloured base-rich surface horizons formed from calcareous parent materials in humid areas mainly under forest. Lithosols were soils with thin, and often irregular, horizons over rock while Regosols were developed mainly from soft or unconsolidated parent materials with or without thin coverings of true soil.

In Soil Taxonomy there are six categories in the hierarcheal system. The basis for the groupings in each category is summarised in Table 3. Low atoll soils will

usually be found in the orders of Entisols (i.e., rec<u>ent</u> soils, having no major diagnostic features), Inceptisols (soils near to point of inc<u>ept</u>ion, showing evidence of profile development beyond that of the Entisols) or Mollisols (base-rich soils having relatively deep dark coloured, organic rich, well-structured surface horizons- the mollic epipedon).

TABLE 3 The Differentiating Characteristics of the Categories in Soil Taxonomy (after Buol et al., 1980)

Category	Nature of Differentiating Characteristics
Order	Soil-forming processes as indicated by presence or absence of major diagnostic horizons.
Suborder	Genetic homogeneity. Subdivision of orders according to presence or absence of properties associated with wetness, soil moisture regimes, major parent material, and vegetational effects as indicated by key properties; organic fibre decomposition stage in Histosols.
Great group	Subdivision of suborders according to similar kind, arrangement, and degree of expression of horizons, with emphasis on upper sequum; base status; soil temperature and moisture regimes; presence or absence of diagnostic layers (plinthite, fragipan, duripan).
Subgroup	Central concept taxa for great group and properties indicating intergradations to other great groups, suborders, and orders; extragradation to "not soil."
Family	Broad soil textural classes averaged over control section or solum; mineralogical classes for dominant mineralogy of solum; soil temperature classes °based on mean annual soil temperature at 50 cm (20 in.) depth§
Series	Kind and arrangement of horizons; colour, texture, structure, consistence, and reaction of horizons; chemical and mineralogical properties of the horizons.

A major difference between the '1938' system and Soil Taxonomy relates to the grouping of soil series into families. The '1938' system introduced soil families as a category between the great soil groups and soil series, but considerable difficulty was encountered in determining what characteristics to use for such groupings. As late as 1949 Riecken and Smith commented "At present there is little published material for guidance in the grouping of series into families". In contrast, Soil Taxonomy has soil families defined as groupings of soil series "having similar physical and chemical properties that affect their management and manipulation for use".

The soils of the low atolls frequently consist of accumulations of organic matter, guano, pumice or other transported material on top of a calcareous sand (calcareous algae, forams, shells, etc.) or limestone substratum. Little profile development has occurred and the development of any significant B horizons is not expected because of the nature of the parent material (calcium carbonate), the relative youth of many low atolls (<5,000 years) and the geographical isolation which has restricted (together with the environment) the development of the flora. Repeated removal of A horizons has occurred on some atolls as a result of cyclones, requiring soil formation to recommence periodically.

As a result the vast majority of soils of the low atolls are Entisols (Soil Survey Staff, 1975) consisting of the accumulation of a thin layer of organic rich coral sand over the coralline substratum. At the suborder level the Entisols are subdivided on the basis of the soil moisture regime or the particle size distribution in the control section (25 cm - 1 m, 25 cm to a lithic contact if one is present within a depth of 1 m). Soils having the groundwater table near the surface have an aquic soil moisture regime and are classified as Aquents.Many atoll soils are sandy i.e. the texture of the fine earth is sand or loamy sand that contains less than 50 per cent very fine sand and rock fragments make up less than 35 per cent by volume (and do not have an aquic soil moisture regime) and qualify as Psamments (Regosols in the '1938' system) at the suborder level. Soils having more than 35 per cent coarse fragments such as coral gravel, stone, and rocks qualify as Orthents (Lithic Regosols or Lithosols in the '1938' system). In both the Psamments and the Orthents the great groups are separated (with the exception of the Quartzipsamments) on the basis of the soil moisture and temperature regimes. The temperature regime for most low atolls is isohyperthermic (i.e., the average annual temperature at 50 cm depth is >22°C, with the variation from summer to winter <5°C), and the soil moisture regimes

in the absence of groundwater influence are ustic (i.e., the soil profile dries out for extended periods in most years) or udic (i.e., the soil profile dries out for only short periods in most years). Thus the great group classifications for the Psamments or Orthents of the low atolls are Ustipsamments or Tropopsamments and Ustorthents and Troporthents. The common subgroups are Typic, Lithic or Aquic.

At the family level all the low atoll Entisols have an isohyperthermic soil temperature regime and carbonatic mineralogy. The Psamments do not require a separate statement of particle size class as this is already designated at the suborder level by the Psamm- prefix; the Orthents have sandy-skeletal particle size class indicating that rock fragments greater than 2 mm make up 35% or more of the volume and there is enough sand to fill intersticies larger than 1 mm. The Aquents usually have a sandy or sandy-skeletal particle size class.

Where the soils have been relatively undisturbed or have had a good vegetation cover for a reasonable time period Mollisols (Soil Survey Staff, 1975) may be found. These are so classified because of the presence of mollic epipedon and the fact that this rests on coral sand where the base saturation will obviously be greater than 50%. A mollic epipedon is characterized by depth, dark colours, high organic matter content, high base saturation, good structure and the presence of sufficient moisture for 3 months or more to facilitate plant growth. The structure of the surface horizons of many low atoll soils is not strong enough to meet the requirements of the mollic epipedon but limited areas of Mollisols have been identified.

The suborders identified on low atolls are Ustolls and Rendolls (Rendzinas in the '1938' system) depending on the soil moisture regime, while the Hapl- great group and Entic subgroup would be expected to be the most common. The family classes are usually sandy or sandy-skeletal, carbonatic, isohyperthermic.

Calcareous soils of low atolls have been studied in a number of locations. The quality and detail of the work varies considerably and it has been difficult in some cases to compare the soils of the different atolls.

1. Tarawa

About 20 pedons in South Tarawa have been classified at the family level in Soil Taxonomy (Seru and Morrison, 1985; Morrison and Seru 1986). The soils generally have

an ustic soil moisture regime, except where there is a marked groundwater influence. The subgroups identified were Typic Ustipsamments, Aquic Ustipsamments, Lithic Ustipsamments (all Regosols) ,Typic Troporthents, Lithic Troporthents (Lithosols), Entic Haplustolls and Typic Tropaquents (wet Regosols). In one area (Bikenibeu) three profiles were found that differed significantly from the others because of the incorporation of organic matter to a considerable depth (found as pockets in the subsurface material) and the associated pockets of material exhibiting structure. The structural features and organic matter incorporation are obviously the result of human activities. One profile showed a fairly uniform incorporation of organic matter (with the associated darker colours) to a depth of about 1 metre. These soils have obviously been subjected to considerable disturbance as they occur in an area of high population and consequent subsistence agricultural activity. This is entirely expected as the Bikenibeu area is one of the most densely populated in the South Pacific.

The classifications of 2 of these profiles as Typic Ustipsamments (Regosols), however, gives no indication of the influence of human activity with the incorporation of organic matter, nutrients and structure to considerable depths in the profile; the third is classified as an Aquic Ustipsamment. These latter features may have considerable agronomic importance in these low atoll soils which otherwise are featureless below the A horizon. The incorporation of organic matter will increase the otherwise low moisture retention capacity at depth. Thus it may be necessary to provide a separate subgroup (Anthropic) of the Ustipsamments for separation of soils which as a result of human activity, have organic materials and associated properties incorporated to depth in the profile.

2. French Polynesia

The soils of a number of low atolls in French Polynesia have been described by Tercinier (1956, 1969) and Jamet (1985). Some of the atoll soils of French Polynesia are considered to have an udic soil moisture regime (C. Garnier, personal communication) and are therefore Tropopsamments (Regosols) and Troporthents (Lithosols) while others have recently been shown to have an ustic soil moisture regime (Service de la Meteorologie, French Polynesia, personal communication) and are therefore, Ustipsamments, Ustorthents with possibly limited areas of Haplustolls.

3. Cook Islands.

The soils of 2 atolls in the Northern Cooks were studied by Bruce (1972). The Muri series was dominant; this is considered to have an udic soil moisture regime and is classified as Typic Tropopsamment (Regosol).

4. Arno Atoll and the Northern Marshalls

The soils of Arno atoll were studied in some detail by Stone (1951) who identified four major soil series. The limited meteorological data indicate that Arno has an estimated annual rainfall >2500 mm and the soils of Arno atoll therefore are considered to have an udic soil moisture regime and the Arno series is thus a Typic Rendoll (Rendzina) and the Shioya series a Typic Tropopsamment (Regosol).

Soils showing surface accumulations of phosphatic material as found in the Jemo series (Fosberg, 1956) were not identified on Tarawa, French Polynesia or in the Cook Islands. However, the Northern Marshalls are considerably drier than the southern group (estimated annual rainfall 1000-2000 mm) and there is a marked dry season November-April leading to the conclusion that they would have an ustic moisture regime. The soils examined in the Northern Marshalls were correlated with those of Arno, (Fosberg, 1956) but in terms of Soil Taxonomy this would now appear inappropriate. A comparison with soils of Tarawa or Christmas Island (Kiritimati) would appear more relevant and the presence of Typic Ustipsamments, Typic Ustorthents and Entic Haplustolls is indicated by the original report (Fosberg, 1956).

5. Christmas Island (Kiritimati), Kiribati

Hammond (1969) produced a detailed report on the soils of Christmas Island. He attempted a correlation with the soils of the Marshall Islands and with the coastal sandy soils of Hawaii. Since Christmas Island has relatively low rainfall (approximately 800 mm annually on average; Taylor, 1973) the soil moisture regime is ustic in the absence of any groundwater influence. Thus comparison with the udic soils of Arno is again inappropriate. The soils of Christmas Island are dominated by Typic Ustipsamments (dry Regosols) but they generally do not have as well developed A horizons as the soils of Tarawa and should therefore be considered as separate series. Analysis of Hammond's report would also indicate that areas of Typic Ustorthents (Lithosols) are also present on Christmas which would correlate with the Bonriki series on Tarawa.

6. Tuvalu

The soils of Tuvalu have received limited study as part of a Land Resources Survey (UNDP, personal communication). The soils have been classified according to the FAO/UNESCO (1974) Legend mainly as Calcaric Regosols; data available in some cases is insufficient to fully classify the soils by Soil Taxonomy. Tuvalu soils have udic soil moisture regimes in the absence of groundwater influence and most will therefore, be Tropopsamments (Regosols) or Troporthents (Lithosols). Insufficient detail on colour and structure prevents the confirmation of mollic epipedons and hence the presence of Mollisols.

7. Ontong Java, Solomon Islands

This isolated low atoll, north of the main Solomon Islands group also has soils that show similarities in morphology to those on Tarawa (Wall and Hansell, 1976). However, the climate on Ontong Java is sufficiently wet to obtain an udic soil moisture regime and the dominant soils are consequently Typic Tropopsamments (Regosols) and Typic Troporthents (Lithosols).

8. Hawaii

The Jaucas series, mapped in coastal sands on several of the Hawaiian islands, is derived from coralline sand and is classified as a Typic Ustipsammment, carbonatic, isohyperthermic (Foote et al.,1972). Examination of the Jaucas data indicates that this soil has a less well developed A horizon than the Abatao series on Tarawa as evidenced by higher values and chromas and lower organic carbon contents. There would appear to be greater similatity between the Jaucas series and the soils of Christmas Island assigned to the Shioya series by Hammond (1969).

9. Micronesia other than the Marshall Islands

Five soil surveys conducted in the Federated States of Micronesia (Laird, 1982; Laird, 1983 a,b; Smith, 1983 a,b) indicate that substantial areas of soils derived from coralline materials are found. These soil series, e.g., Ngedebus, Insak, Dublon have an udic or perudic (i.e., soil profile never dries out to any extent) soil moisture regime as the rainfall in the area ranges from 3000-5000 mm annually with no marked dry season. The coralline soils have therefore been classified in the Tropo- great groups of Entisols rather than in Usti- great groups.

Thus it can be seen that the dominant soils of the low atolls are Entisols, being mainly classified in the Psamments or Orthents suborder. Trop- and Ust- great groups occur depending on the soil moisture regime. Limited areas of Aquents and Mollisols may also be found.

SOILS OF THE RAISED ATOLLS

As the soils of the raised atolls show considerably greater variation than is found in the low atolls, the individual islands will be considered separately.

Lifou, in the Loyalty Islands of New Caledonia is a raised atoll of area 1,149 km^2. The proximity of the volcanic zones of Vanuatu has led to the deposition of substantial quantities of pyroclastic materials on the limestone. These pyroclastic materials have weathered to give products of the allophane family in the youngest deposits and bauxitic materials in the oldest deposits. Three major soil environments have been identified (Latham, 1981).

On the west coast, steep cliffs of a rampart overhang a narrow coral sandy beach. On the rampart a karstic microrelief is found; organic matter accumulates giving soils up to 1 m deep in the deepest pockets. Within the former lagoon two soil series are found. One is a shallow calcareous soil with an organic rich surface layer but of variable depth (Lithic Troporthent or Lithosol). The other is a red-brown oxide rich soil of 30-80 cm depth resting on the limestone. On the east (windward) coast there is a a coastal plain 100-200 m wide with sandy or gravelly soils containing large quantities of pumice. They are rich in organic matter which accumulates to a depth of 30-50 cm. These are fertile soils and many crops thrive on them if sheltered from the prevailing winds. On the coastal plains, silicate - containing breakdown products of the allophane family have been identified, but on the rampart and in the old lagoon the non-calcareous materials are geologically older and have lost all the silica to give soils dominated by gibbsite, boehmite, haematite and goethite.

These oxidic soils are of variable depth, but cover a major part of the surface of the island. They have pH values from 6-7.5 and have high levels of organic matter (often >10% for topsoils) under natural vegetation. In the absence of silicate clay minerals, adsorption and availability of nutrients is dependent on the organic matter content. CEC values are correlated to organic matter levels. Exchangeable base contents are reasonable in the topsoils, but are often very low in subsoils (sum

of bases <1.5 cmol/kg) and potassium levels are frequently particularly low (<0.1 cmol/kg). Water retention is greater than on the low atolls as the oxides contribute along with the organic matter to this property. Zinc, manganese and boron deficiencies have been observed and silicon deficiency is expected for crops like cereals that require significant quantities of this element.

The classification of these soils presents problems. Several have a mollic epipedon overlying an oxide rich subsoil where the CEC is near the borderline for the oxic horizon. In the subsoils the base saturation is frequently low so those soils that do not qualify as Oxisols (Typic Acrustox - Laterite soils in '1938' system) are often Oxic Humitropepts (Latosols in '1938' system). Latham (1982) has argued that the Typic Acrustox classification does not give any indication of the presence of substantial quantitites of organic matter.

Nauru is a raised atoll (0°32'S, 167°03'W) of 22.6 km^2 with its highest point approximately 70 m above mean sea level. The limestone has been covered with a substantial deposit of phosphatic material, the origin of which has not yet been fully explained. The soils of Nauru are being rapidly removed by phosphate mining operations. A stockpile of topsoil is being accumulated and, after the completion of mining activities around 1995 A.D., may be spread over a limited area and used for small scale agricultural production to support the remaining population. The terrain remaining after mining is so rugged that an extensive agricultural development would be prohibitively expensive.

A recent study has been made of the soils in areas remaining undisturbed (Manner and Morrison, unpublished data). Three separate soil series occupying significant areas have been identified. The first series has a dark epipedon overlying a layer of mixed surface material and broken limestone, which in turn lies on limestone rock. This profile has been classified as a Lithic Haplustoll (Rendzina in '1938' system). The second series has a thin (<10 cm) dark epipedon directly overlying the limestone substratum and is classified as Lithic Ustorthent (Lithosol). The third series occurs in areas where the phosphatic material has accumulated between limestone pinnacles. The phosphatic material is frequently reddish yellow (7.5 YR 7/4) coloured between 25 cm and 75 cm depth, changing to pinkish gray (5 YR 7/2) colour at greater depths. The Bw horizon is occasionally stony or bouldery with lumps of limestone occurring throughout. Soils of this third series have epipedons that meet the criteria for mollic, and have therefore, been classified

as Typic Haplustolls. There are limited areas of shallow sand deposits, particularly near the coast, on which Lithic Ustipsamments (Regosols) or Ustorthents (Lithosols) have formed. In the very limited wet areas close to the old lagoon shallow Tropaquents (Hydromorphic soils) are found.

Chemical data from the analyses of some 50 Nauru soil samples (Morrison and Manner, unpublished data) show that the soils usually have pH (H_2O) values from 6.0 - 8.0, pH (KCl) values from 5.5 - 7.8 and free calcium carbonate was found in all samples, the extent varying from 2-24%, being highest in subsoils. Organic carbon contents ranged from 1-11% for topsoils, the values varying widely with the impact of mining. For subsoils the values from 0.1-1.9%, decreasing with depth in undisturbed profiles but varying significantly within the mined areas. C:N ratios for topsoils ranged from 7-24 with the highest values being found on highly disturbed sites. CEC values for topsoils varied from 12-61 cmol/kg, while for subsoils the range was 4-21 cmol/kg. There was a reasonable correlation between CEC and organic matter contents. Exchangeable magnesium values ranged from 5-14 cmol/kg for topsoils and from 0.1-3 cmol/kg for subsoils while exchangeable potassium values were uniformly low (< 0.5 cmol/kg). Total phosphorus levels varied from 2-18%, the lowest values being found in soils on the fringing reef surrounding the island. Phosphate extractable sulphate values varied from <1-90 mg/kg, but most values were < 20 mg/kg. The highest values were found for undisturbed forest soils.

Mineralogical analysis of a limited number of samples showed a dominance of fluoroapatite and hydroxyapatite with limited amounts of calcite and aragonite in the soils of the fringing reef surrounding the island. The apatites appeared very pure and carbonate-apatite was not detected in any samples (Morrison, unpublished data). It is interesting to note that one sample from Makatea in French Polynesia (where phosphate deposits are also located) gave effectively an identical mineralogy to the Nauru samples. The mineralogy class of most Nauru soils is mixed according to the criteria given in Soil Taxonomy but it would appear that the use of phosphatic or apatitic would be more appropriate.

A major problem that has arisen in the classification of soils of Nauru is the determination of the soil moisture regime. No direct measurements of soil moisture are available and the estimation of soil moisture regimes has to be based on meteorological data. Data for Nauru (40 years) show a mean annual precipitation of 2000 mm

with 4 months having rainfall below 100 mm. Annual rainfall has, however, varied from 280 mm to 4500 mm. Air temperatures range from 23-32°C with the relative humidity averaging 71%. Nauru is periodically affected by droughts and several droughts of more than 12 months duration have been recorded this century. However, taking the average rainfall data available and assuming evapotranspiration rates averaging 4 mm per day in the non-drought years it would appear that the soils of Nauru not influenced by the effects of groundwater fit best into the ustic moisture regime (udic tropustic in the tentative sub-divisions of moisture regimes proposed by ICOMMORT (Van Wambeke, 1981)).

The soils of Niue (19°S, 169°54'W), a raised atoll of area 259 km^2 have been extensively studied (Wright and Van Westerndorp, 1965; Leslie, 1985). The rocks at the surface and around the cliff coastline are all coral reef limestone. There is considerable evidence of past changes in sea level, with shelly and soft makatea* forms in certain areas of the island, indicating that the sea probably covered all of the island at some time. The limestone and makatea have been covered by a thin layer of submarine sedimentary material (P. Rankin, personal communication). Thus limestone, makatea and sedimentary materials are the parent materials for Niuean soils. The sedimentary material has been very strongly weathered and has virtually all been converted to oxides.

The basic soil pattern is basically a concentric set of the main soil groups with a more complicated pattern existing within the broader one due in part to the occurence of makatea or coral limestone pinnacled outcrops. Three orders of Soil Taxonomy (Soil Survey Staff, 1975) have been identified on Niue. The Fonuakula series with an oxic horizon is found in areas of deeper accumulation of the highly weathered sedimentary material. This soil meets the criteria for an Oxisol and since Niue has an ustic soil moisture regime and an isohyperthermic soil temperature regime is placed in the Ustox suborder. Since the base saturation in the major part of the oxic horizon is greater than 50% the Fonuakula series meets the

* makatea: A raised reef becomes severely eroded with long exposure because of the solubility of the limestone in rainwater. The surface becomes rough, rugged, full of pinnacles and solution holes and the limestone becomes cavernous and porous. This landform is called 'makatea' in Polynesia (literally 'white rock' or 'white cliff').

requirements for inclusion in the Eutrustox great group and is a Typic Eutrustox (Laterite soils in the '1938' system). The family designation is clayey, gibbsitic, isohyperthermic.

Two soil series, Avatele and Tafolomahina, are classified as Ustropepts (Latosols in '1938' system) at the great group level on account of having ochric epipedons and cambic horizons and base saturation greater than 50% in all horizons. The Avatele satisfies criteria for Typic Ustropepts (family designation fine, oxidic calcareous, isohyperthermic), while the Tafolomahina soils having a Lithic contact within 50 cm of the soil surface and a relatively low CEC (< 24 cmol/kg) are classified as very-fine, gibbsitic, Oxic Lithic Ustropepts.

The great majority of the soils of Niue are Mollisols (10 out of 13 series) in that they have mollic epipedons overlying base-rich subsurface materials. At the suborder level they are all Ustolls (Niue has an ustic soil moisture regime) and are classified as Haplustolls at the great group level since they lack other diagnostic features. However, none meet the criteria defined for the Typic subgroup of Haplustolls. Some lack soft powdery lime and are therefore Udic Haplustolls, others lack soft powdery lime and do not have a cambic horizon and are therefore Udorthentic Haplustolls. The presence of lithic contacts within 50 cm leads, together with other criteria to including series in the Lithic Ruptic-Entic and Ruptic-Lithic Udorthentic subgroups. Low CEC values in the subsoils of some series lead together with other data to their inclusion in the Oxic Udorthentic and Oxic Ruptic-Lithic Udorthentic subgroups.

Most of the soils of Niue are strongly weathered and the dominant minerals are gibbsite, goethite and crandallite $(Ca, Sr, Pb)_2Al_7(PO_4)_3(OH)_{16}.3H_2O$ with a virtual absence of silicate materials. The presence of large amounts of crandallite in some soils has led Leslie (1985) to propose that a crandallitic mineralogy class be established in Soil Taxonomy. To qualify for designation as having a crandallitic soil mineralogy class soils would have to contain more than half crandallite by weight in the control section.

Micronutrient deficiencies have been identified in a number of crops grown on Niue (Miller, 1980). The highly weathered nature of the Niue soils means that those that are not calcareous (having similar problems to those of low atoll soils discussed earlier) are oxidic or crandallitic being dominated by materials having extremely

limited supplies of trace elements like zinc and manganese required for good crop production.

CONCLUSION

In this paper information on soils of some low and raised atolls in the South Pacific has been reviewed. For the low atolls many similarities are observed in that the soils show minimal profile development and are highly calcareous and highly dependent on organic matter for moisture and nutrient retention and availability. The soils are usually Entisols (Regosols or Lithosols), the major differences being in the soil moisture regime and the particle size class. Micronutrient and potassium deficiencies are encountered widely.

The raised atolls show much greater variability in soils due at least in part to the additions of non-calcareous materials. The soil patterns are usually more complex than on the low atolls. While Soil Taxonomy can be utilized quite successfully in the classification of atoll soils some modifications may be required to fully accommodate this unique group of small island soils.

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ATOLL RESEARCH BULLETIN

NO. 340

POPULATION PRESSURE ON CORAL ATOLLS: TRENDS AND APPROACHING LIMITS

BY

MOSHE RAPAPORT

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ABSTRACT

Coral atolls are oases amidst an oceanic desert. However, most are extremely isolated and are subject to natural hazards, and are covered by barren coral rubble with a vulnerable fresh water lens. Atoll production systems include tree crops, root crops, fisheries, mariculture, and cottage industries; some atolls have experimented with commercial fisheries and tourism. Land is generally equitably distributed. Atoll communities are substantially dependent on metropolitan powers and high islands. The dependent groups have smaller populations, low growth rates, higher per capita aid, emigration privileges, and minimal urbanization. Independent groups appear to be closest to their carrying capacities. Regional disparities in population distribution can be explained by an analysis of carrying capacity. The proposed model begins with increased expectations and perceived needs. This results in migration from outer islands and signs of population pressure in district centers; leading to urbanization, emigration, and carrying capacity overshoot in both the region and overseas.

INTRODUCTION

Atolls are island studded coral rings surrounding clear, deep lagoons. They are remnants of volcanic islands which have now sunk thousands of feet below the surface of the sea. They are located in archipelagoes, clusters, and as single isolates scattered across the oceans. The great majority of them occur in the Pacific, though there are also many in the Indian Ocean. They are rich, mutually supporting, and self-sustaining communities of marine and

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terrestrial organisms, and are one of the great miracles of nature.

The equilibrium of interacting living communities on atolls is balanced precariously and is periodically disturbed by drought, hurricanes, and tidal waves. Most atolls support human populations, typically numbering in the hundreds. However, human existence on atolls does not have the safety margin available in continental and large insular regions. There are usually only a few square miles of land area; in some cases, less than a single square mile. Considerable effort is needed for exploitation of atoll soils which are poor in available plant nutrents, and subject to periodic drought, deluge, and salt inundation. Although reefs can sustain a large animal biomass, they can be adversely affected by human population density. Marine resources are relatively abundant, but are dependent on the skills and technology available to local populations.

Both population pressure and the resulting intensification of use of natural resources can eventually erode the land; pollute the soils, reefs, and lagoons; and endanger a uniquely balanced biotic community which is perfectly adapted to the atoll habitat. The growing demand for outboard engines, chemical fertilizer, and industrial development poses threats to the natural environment even if population were to remain stable. Finally, intervention by external political influences have played a role in the changing of atoll society. Thus, any discussion of the implications of population pressure must also consider the effects of urbanization and foreign relations.

This study provides an analysis of population-environment relations on the major atoll groups. It first considers the indigenous resources, production systems, and resource distribution. This is followed by a review of demographic trends including population growth, migration, urbanization, and political dependency. The concept of human carrying capacity is explored. Traditional models are criticized because of their inability to account for external linkages. The proposed approach assumes a dynamic carrying capacity based on perceived needs and overseas linkages; explains regional disparities in population distribution; and provides a continuing model for population movement from outer islands to district centers and mainland areas.

THE ATOLL ENVIRONMENT

Physical Geography

Some of the most important environmental studies of

coral atolls have been conducted in the preparation for atomic testing in the former U.S. Trust Territory of the Pacific Islands. In response to a request from the South Pacific Commission, many expeditions were sent out by the Pacific Science Board, a branch of the National Research Council of the National Academy of Sciences. Interdisciplinary physical and biological studies of atoll lands, reefs, and lagoons were carried out. Many of these studies have been published in the Atoll Research Bulletin. A major contribution was also made by Wiens (1962) who compiled a useful volume on atoll environment and ecology based on the previous research. The following description is indebted to these studies.

Atolls are generally described as oval shaped coral reefs surrounding a lagoon in which there are no islands except for slightly submerged reefs. According to current theory, atolls were formed by subsidence of a volcanic island and the gradual rise of the fringing reef. Present living reefs veneer a much older surface in part marked by glacial and interglacial sea level fluctuations. In <u>true</u> atolls there is complete subsidence of the oceanic island; in <u>almost</u> atolls, volcanic peaks remain as islands within the lagoon; in <u>raised</u> atolls, the reef is raised considerably above sea level through tectonic processes. The highest point on an islet is usually no more than 10-15 feet above sea level. It typically occurs at a coral rubble ridge located on the ocean side of an islet and is built up by storm waves over many years from sediment produced by erosion during major storms of the outer reefs. Finer sediments occur in the lee of the rubble ridge. The interior of an islet is covered by a surface of coral rubble or sand in which a variety of drought and salinity resistant species of land plants can take hold. Like all islands, they are colonized by drift and by migrating seabirds. The natural atoll forest is dominated by species such as <u>Pisonia</u>, <u>Tournefortia</u>, <u>Guettarda</u>, <u>Cordia</u>, and other species, forming a canopy forest. <u>Cocos</u>, <u>Artocarpus</u>, <u>Cyrtosperma</u>, and perhaps <u>Pandanus</u>, have been introduced to most inhabited atolls. Approaching the lagoon side of the islets, the coral rubble becomes increasingly finer until at the lagoon beach it is usually composed of fine sand.

Atoll long axis lengths range from about twenty miles or more, to five or less. The largest lengths occur in the Marshalls, the Tuamotus, and the Maldives. Between the islets, the reefs are submerged only a few feet, and can usually be easily traversed by foot during low tides. Some third of all atolls have a deep, natural channel across the reef, allowing for the passage of boats, sharks, and large fish into the lagoon. Lagoons are generally shallow in the small atolls (less than 25 fathoms) and are deeper in the

wide atolls (typically ranging from 30 to 45 fathoms). Patch reefs are present inside the lagoons and are important for the associated assemblage of coral, clams, crustaceans, eels, and fish. The large atolls more frequently have passes and are rich in their lagoon fisheries potential. Small atolls have to rely to a greater extent on hazardous open sea fisheries.

Most atolls are subject to periodic droughts and severe storms, but a few face extreme environmental challenges. In particular, the Northern Marshalls, the Southern Gilberts, the Line Islands, and the Phoenix Islands (Kiribati) are prone to severe periodic droughts. Western Micronesia is prone to hurricanes more often than some of the others. Atolls can be affected by devastating tsunamis and wave trains from major storm centers which can propagate for thousands of miles from their source. Atolls subject to these natural hazards have a very small margin for carrying capacity. Following severe storms and droughts, coconuts, breadfruit, and taro pits may take years to recover. Reconstruction of housing, water catchment sites, and public buildings can be a severe drain on labor, income, and natural materials.

Fresh water is the most limiting requirement for settlement on atolls. Islet material is generally so porous that drainage by percolation occurs almost instantaneously. Some water is held in capillary openings in the soil and remains available to shallow rooted plants. The surplus seeps down to a lens of fresh water saturating rock and sand. The shape of the lens depends on local geologic conditions, shape of the islet, tidal movements, and inputs of rainfall. Today, atoll societies rely on ground water and catchment, but in previous times some atoll communities survived solely on coconut water and occasional water collection in excavated coconut trunks. Most atoll plants can survive on the periodic moisture in the unsaturated zone of the soil but taro, bananas, and breadfruit require the presence of ground water. Coconut and pandanus can survive without ground water but do best in wet climates.

Human effects on the reef in previous times have generally been minimal. However, today, a variety of development related projects are likely to have a deleterious effect on the reef system. Reef blasting for boat channels is suspected to be linked to ecological disturbances favoring the spread of ciguatera and other problems. Mining the reef for construction material may cause even more extensive damage. Urbanization can cause depletion of species and contamination of the lagoon. Since initial settlement, human effects on the land have been significant on virtually every atoll group. The natural

forest has largely been replaced by introduced species, while copra export and loss of seabird nesting colonies have led to soil depletion of potash and other elements. Copra has brought greater security in food supplies and eased man's labor in many respects but recent price fluctuations have endangered even this resource.

Production Systems

Data on productivity and yield of indigenous Pacific Island production systems are extremely limited. Regional studies in the South Pacific (Ward and Proctor, 1980) and the North Pacific (U.S. Congress, 1987 and Mark, 1982) have mainly been concerned with reviews of high island production systems. Notable exceptions include the South Pacific Commission Conference on Atolls (S.P.C., 1982; and numerous unpublished papers), the UNDP Integrated Atoll Development Project (Liew, 1986), and the ongoing UNESCO Man and the Biosphere Project. There have also been important studies of traditional fisheries (Johannes, 1981), tuna fisheries (see S.P.C., 1981), and subsistence agriculture (University of Hawaii SPRAD Program).

A variety of marine resources are available on atolls and probably were the major source of food for the initial colonists. Even today fish is the major item of diet on many atolls, and after a major storm, tidal wave, or drought, when most of the terrestrial reserves can be devastated, life continues by relying on the sea. Reef, lagoon, and sea organisms are diet staples on all atolls and include crabs, fish, clams, eels, turtles, octopi, holothurians, and even worms. Atoll fishermen have an extraordinarily detailed knowledge of fish ecology and habits. Yield has further improved--though often at the cost of resource depletion--as a result of modern nets, spearguns, nylon line, and outboard motors.

An excellent review of fisheries potential is provided by Salvat (1980): Productivity is limited by the absence of continental shelves, shallow lagoons, no important zones of upwelling, little input from land drainage, deep thermoclines, relatively barren oceans, and increasing international exploitation. In the midst of this oceanic desert, the coral reef ecosystem is among the most productive on earth and is sustained by symbiotic relationships which keep energy loss to a minimum. Fisheries on the small islands have traditionally relied primarily on the reef and lagoon resources but there is currently interest in increased exploitation of both the outer reef slopes and the surrounding ocean.

Reef and lagoon fish are characterized by great species

diversity and small sizes of edible fish, which does not favor commercial production. The presence of coral heads also favors the use of individualized fishing methods such as lines, traps, nets, drives, and spears. Species caught belong to the families Siganidae, Serranidae, Carangidae, Lethrinidae, Acanthuridae, Ballistidae, Exocotidae, Mullidae, Mugilidae, and many others. Intensification of fisheries using modern methods leads to stock depletion since most reef species tend to be highly territorial. Introduced methods have already severely damaged the lagoon ecosystem in some atolls. Constraints are also posed by the prevalence of fish toxicity and vulnerability to pollution. Other reef genera that have been traditionally exploited include Pinctada, Tridacna, Trochus, and Holothuria. These can all be an important source of income for atolls, though pearl farming may require the right conditions and substantial investment.

Outer slopes of atolls typically descend at steep angles to the ocean floor. There is little live coral below fifteen fathoms but there is a substantial amount of demersal fish including Lutjanus, Pristopomoides, Aprion, and others. These are large fish which live at great depths and can also be caught by individual fishermen in small canoes. However, they are often underexploited because of the lack of the means and knowledge to work these depths. Deep sea resources include Thunnus, Katsuwonus, Acanthocybium, and others. Traditional deep sea fishing (trolling with lure or fish) was often an incidental activity of interisland voyaging but it is now becoming increasingly commercialized using a variety of modern methods (see Salvat, 1980). There is believed to still be considerable room for expansion of the skipjack fisheries (S.P.C., 1981).

Terrestrial resources are considerably more limited than marine resources. Atoll soils are composed almost entirely of calcium and magnesium carbonate, and are derived primarily from coral and calcareous algae, and also from shells and foraminifera. Iron, nitrogen, and other mineral elements are deficient. This poses severe limitations on horticulture. The coconut is the most important tree on atolls and the majority of land is devoted to it. Human populations are dependent on the coconut for food, drink, fuel, construction, and textiles. The availability of coconuts has increased as a result of the copra trade as well as the imposition of peace during the colonial period (Wiens, 1962). However, production is limited by neglect and overcrowding, partly due to copra price fluctuations. Breadfruit is also a very important source of food. It does not require high rainfall and is found even in the Northern Marshalls (Pollock, 1970). It tolerates salinity poorly and

is generally planted on the lagoon side and interior of the islet. Pandanus is part of the indigenous forest system and is utilized for food, textiles, and handicraft production. A large variety of the above species are cultivated but have been incompletely documented in the scientific literature.

While Colocasia is cultivated on some of the wetter atolls, Cyrtosperma (pit-taro) is the traditional root crop on most atolls. It is nutritionally superior to white flour and rice, can be produced indigenously without foreign technology, and is especially important for feasts and ceremonial occasions. Pits are dug down to the fresh water lens, a compost of leaves is added, and a muck soil is produced that can be sustained indefinitely. Cyrtosperma is relatively disease resistant compared to other taros. However, the work is labor intensive and the tubers may require a lengthy maturation period (Bayliss-Smith, 1980). It requires lengthy hours of work, often while being harassed by mosquitos. Its production has unfortunately declined in most atolls. In some cases, this was due to infestations of leaf blight and weed introductions. In other areas, epidemics, social breakdown, and extensive copra plantation may have been responsible (Thaman, 1984). The impacts of natural hazards and foreign dependency can also not be discounted. Probably the major reason for their neglect is the fact that their productivities cannot compete with the returns usually available from the commercial economy (Bayliss-Smith, 1986).

Traditionally, atoll communities practiced numerous conservation and management strategies. Some of these are listed by Liew (1986). One of the most important practices was the imposition of periodic taboos on plantations and on reefs. Other practices included size limitations for certain species; cooperative sharing of swordfish, turtles, and large fish catches during the spawning season; quota systems for families and kin groups; and preservation of forest groves and tabu islets for canoe building, construction, bird nesting, and religious purposes. With the decline of traditional authorities, and with the greater reliance on external inputs (eroding the perceived need for self-sufficiency), these regulations have weakened or been lost altogether.

In his survey of Ontong Java, Bayliss-Smith (1986) finds that in order to cope with an expanding population, the atoll society will have to respond with full use of subsistence resources, an intensification of copra making, or further exploitation of holothuria. He notes that most subsistence activities are labor demanding and are already close to being fully utilized. Because of the substitution effect of the commercial economy and decreasing tolerance of

an unmodified traditional diet, further erosion of self-sufficiency is expected. Unfortunately, he adds, there is no forseeable increase in local income in the near future.

Because of the price instability, decreasing value, and susceptability to natural hazards of copra production, and the limited potential for atoll agriculture and handicraft production, alternative modes of production have been proposed (see U.S. Congress, 1987). Commercial export fisheries and tourism have been successfully implemented in the Maldives and now provide the major source of income for a large atoll population that receives much less development aid than other atoll groups. These ventures have been reviewed by a World Bank economic survey (World Bank, 1980). The fisheries industry is handled and marketed by Japanese companies with sophisticated collection vessels moving from atoll to atoll with freezer facilities. The fisheries sector now accounts for one third of the GDP, almost half of all employment, and nearly all visible export earnings. Tourism exists in the form of resorts on outer islets of the main atoll. Because of their location, there has been minimal deleterious cultural effect on the islanders. It accounts for a tenth of the GDP and is the most important foreign exchange earner.

These industries are being increasingly investigated as options in the Pacific because they have been demonstrated to reduce the reliance on unstable aid, generate employment for land-poor persons, outer islanders, and urban populations, and stimulation of other sectors, including agriculture. However, their applicability to the Pacific region is questionable (Castle, 1980). The remoteness of Pacific atolls greatly adds to transport expenses. Smaller populations and reef areas do not allow for the economies of scale available in the Maldives. There may also be some major societal costs for industrial development that is not carefully regulated, including the likelihood of class division and environmental degradation.

Resource Distribution

Atoll societies have typically been very egalitarian (see Sahlins, 1971). Extended families shared fish that were caught, often cooperated in other subsistence activities, and helped with construction projects. Frisbie (1921) provides a first hand description of a traditional atoll society:

> "Puka-Puka is, perhaps, the only example on earth of a successful communistic government. . .Here there is no private ownership of lands other than the tracts upon which the houses are built, and even in this case the land really belongs to the villages, which give the

> residents unlimited lease to live thereon. When the villagers move for a few weeks sojourn on their respective islets, the coconuts are gathered, stacked in the temporary village, and then equally divided among the men and women, a small share being reserved for the children. The nuts are then opened and dried for copra. . .The money received is either divided equally among the villagers or used to purchase clothing, tobacco. . .which is then divided. Likewise, when it is found that the puka trees are full of young birds, the men catch them and the same division takes place. Even the fishing is often managed in this manner. . . Of course, if they had the slightest taint of ambition, their system would fail, for under it, it is quite impossible for one man to be richer than another. When, in the course of decades or generations, some unnatural go-getter happens to be born, he soon finds life so intolerable that he emigrates to an island where communism doesn't prevail. But Puka-Pukans, with very few exceptions, are wholly satisfied with their system. They avoid all land disputes, and no one is faced with the problem of how to make a better appearance in the world than his neighbor."

Other Pacific atolls are also generally less hierarchical and more egalitarian than their large insular counterparts (See for example, Sahlins, 1971; Pollock, 1970; Alkire, 1978; Chambers, 1982; and Bayliss-Smith, 1986).

Although cooperative stores have been successfully introduced to many atolls (see for example, Howard, Plange, Durutalo, and Witton, 1982; and Geddes et al, 1982), there is increasing decline of the cooperative ethic as a wage based economy replaces the traditional subsistence lifestyle. Cash income is used to purchase imported food, fuel, clothing, construction materials, and outboard engines. Profits from fishing and diving are becoming increasingly restricted to families with government employment who can afford the necessary equipment (Bayliss-Smith, 1986). There is also a tendency towards individualization of land tenure, a shift to the nuclear family system, and urban/rural social distancing (Ward and Proctor, 1980). In the subsistence economy, there was little need for excess acquisition of land by any one individual or family. As land--as well as labor--acquires an exchange value, there is a trend towards alienation by entrepreneurs.

This trend has received encouragement by some scholars. In a study sponsored by the U.S. Congress, Mark (1982) advocates increased land use controls including property taxes in order to "increase the efficiency of the present

real estate market and thereby facilitate the transfer and consolidation of parcels for agricultural use." Similarly, Crocombe (1971) notes that increased yield may be obtained under individualized tenure and even greater yield possible using industrial methods designed to maximize production. Both Mark and Crocombe refer primarily to the high islands, but the arguments are likely to be supported in the atolls as well. Although Geddes et al (1982) correctly note that land reform is not generally needed on most atolls, there is a definite trend which may ultimately lead to serious maldistribution in the not too distant future. Better technology, the availability of mechanized transport, the possibility of absentee ownership, distant political administration, codification of tenure rights, increasing immigration and emigration, and urbanization, are all acting to foster maldistribution of land and other resources in many part of the Pacific (Crocombe, 1971). Preservation of traditional tenure systems may also be desirable in view of the surprisingly high productivity in some areas.

Maldistribution is particularly problematic in the Maldives. In this Indian Ocean atoll group, with a trading and mercantile history dating back over a thousand years, wealth is overwhelmingly concentrated in the hands of a few families in the capital. Land is officially owned by the state but it is leased to private developers who exploit the land without regard to long term environmental consequences, resulting in a large class of land poor residents, with adverse consequences to the health of both the population and the environment. Unfortunately, once alienation has been accomplished, it is quite difficult to reverse. Crocombe (1971) correctly notes that political elites may publicly support land reform because the voters want it; but in private, and in practice, they oppose it because reform would deprive them of their political and economic power.

SUMMARY

Atolls have limited land area, scarce water supplies, barren soils, and a vulnerable ecosystem. They are subject to hurricanes, tsunamis, and droughts; and may even be innundated by rising sea levels in future years. Atoll societies have traditionally survived on subsistence fisheries and horticulture. A great diversity of foods is available in lagoons, reef flats, near shore waters, and the deep seas. Horticulture is generally limited to pit-taro, coconuts, and breadfruit. In most areas, a level of subsistence-affluence could be maintained through use of resource conservation. However, these constraints are currently in decline. Both reefs and land are becoming increasingly endangered by new exploitation technologies, population pressure, urbanization, blasting, reef mining,

forest clearing, and erosion. Industrial enterprises are being investigated in some areas but the environmental and cultural costs may outweigh the benefits.

ATOLL POPULATIONS

Contemporary Trends

Many Pacific atolls once supported larger populations than they do today. This does not, however, imply the desirability of restoring these population levels in the atolls. Early accounts often indicated a "miserable existence for the inhabitants of many atolls visited" (Wiens, 1962). Social taboos and restrictions were necessary in historical times and these were often inadequate, leading to starvation, emigration, and war (Alkire, 1978 and Pollock, 1970). What is the situation like today?

Satisfactory analysis of the problem of population pressure on food and other atoll resources has been difficult to achieve because of limited cartographic anddemographic data as well as methodological problems in the areal estimation of productivity of land and reef. It is clear, however, that improved medical supplies, education, and sanitation are decreasing mortality rates while the cultural controls on birth have largely been removed due to missionary influence. In spite of migration to high islands and mainland countries, on many atolls there is an increasing population pressure upon resources. Rising populations, intensified exploitation of resources, and increasing pollution of an extremely fragile and limited environment is likely to negatively affect long range carrying capacity (see Alkire, 1978; Connell, 1983).

It is difficult to appreciate the implications of population pressure on an atoll without having been there. Crowding in a community on a tiny islet is a much more socially intense situation than denser crowding in a town in the midst of open country. These effects are rarely described in statistical studies, but are important for an understanding of the meaning of population pressure. An anecdotal example may thus be appropriate. Fale is the main village of Fakaofo Atoll in the Tokelau Islands. The village is located on an islet of eleven acres. The houses are clustered right next to each other and right down to the water. There are no beaches because the land has been extended by sea walls for construction purposes. There is no empty space in the village except for the small clearing in the village center and a rocky peninsula with pig pens. Young people who would like to meet alone in the evening must go to extraordinary lengths to find some privacy, often

using the pig pens or even the over water latrines! A U.N. volunteer living on the islet referred to it as a "pressure cooker."

Emigration to urban areas on atolls (e.g. Majuro, Tarawa) has resulted in lawlessness, drunkeness, and social disintegration, leading to an increasing dependence on foreign aid (Connell, 1983). It has in some cases resulted in squatter settlements on the fringes of the main atoll center which are subject to discrimination by the larger community. In good times, remittances are sent to outer island relatives which further attract migrants. In bad times, migrants are a drain on their home islands. The loss of able bodied persons--to the economic and social incentives provided by urban centers--may leave the outer islands with insufficent labor, acts as a disincentive to subsistence agriculture and fisheries, and places a strain on the island communities. Subsidized medical care, shipping, schooling, and food supplies may be necessary to maintain outlying communities that can no longer engage in subsistence activities (see Yen, 1980). Modern transportation has furthermore had the paradoxical effect of increasing isolation between neighboring islands which formerly relied on continuous interisland canoe voyaging (Proctor, 1980).

Alkire (1978) predicts that unless there is a revitalization of subsistence horticulture and maritime exploitation, there is a very real possibility that the standards of living for coral islanders will further decline. The only other options are increased subsidization and emigration. (He notes, however, that coral islanders have previously survived resource shortages and population displacements by adaptive strategies that maximized options.) Similarly, Bayliss-Smith (1986) notes that in Ontong Java, population projections and carrying capacity calculations show that severe strains on island resources are likely within ten years. Concern about imminent population pressure has also been raised in the Marshalls (Pollock, 1970), Kiribati and Tuvalu (Geddes et al, 1982), the Maldives (World Bank, 1980), and many other atoll groups (Connell, 1983).

Population growth is widely believed to have adverse consequences for economic growth (Coale and Hoover, 1958; McNamara, 1977). This position has been challenged by some who believe that population growth may be beneficial since it results in economies of scale and promotes technological progress (Boserup, 1981; Simon, 1977, 1981). Similarly, the argument that population growth leads to emigration and unmanageable urbanization has been challenged on the grounds that rapid population growth can in fact decrease the rate

of urbanization by the increased supply and decreased value of labor; while promoting agriculture, which can be intensified. This effect is--arguably-- reinforced by the higher demand for food associated with population growth (see Ahlberg, 1986). Natural limits to urban growth are postulated to be related to increasing urban "disamenities" (crowding, crime, and health problems). However, on atolls, it is likely that even the pro-growth theorists would advocate caution.

The following sections will present a demographic survey of the major atoll groups. They are divided into two super-groups, based on political dependence, an important criterion which will be seen to be linked with population pressure, urbanization, and other variables. The large group of atolls in the Federated States of Micronesia are considered dependent because they are administered from four high island district centers whose environment and society is quite different from outer island settlements. The Marshall Islands are considered independent since they are not governed by a high island or metropolitan country. The Tuamotu Archipelago is dependent since it is externally administered. The data used excludes the high, volcanic islands of Micronesia, but some of the raised atolls in Micronesia and the Tuamotus were included in the aggregated data. The data for the Tuamotus also includes the Gambier Group which was aggregated with the Tuamotus in demographic surveys. The comparisons are based on census data from 1977-83, which have been compiled in Connell (1983), the Pacific Islands Year Book (1984), and the World Bank (1980).

Dependent Groups

The dependent atoll groups include (in order of increasing population size) the Tokelau Islands, the Northern Cook Islands, the Tuamotu Archipelago, and the Federated States of Micronesia. These groups generally have low total populations compared to the independent groups. Average population per atoll in all groups is a few hundred persons. Overseas development aid per capita is generally higher than in the independent groups. There is little urbanization since district centers are located outside of these atolls (table 1). Population levels are generally stable (table 2).

Tokelau is a group of three atolls in close proximity to each other about three hundred miles north of Western Samoa. The atolls are small, but there is adequate rainfall. It is a territory of New Zealand and is administered jointly by a council of elders on each atoll, a Tokelauan public service office in Apia, Western Samoa, and the New Zealand Ministry of Foreign Affairs. It is perhaps the most conservative and

traditional of all the atoll groups in the Pacific. Private enterprise and tourism are discouraged. A subsistence economy based largely on fisheries and coconuts is supplemented by aid, remittances, government employment, philatelic sales, and handicrafts. There are high rates of natural increase, relieved only by migration to New Zealand, where migrants have become fairly well integrated into the society, and are important contributors to the labor force.

The Northern Cooks are scattered from each other by considerable distances and from Rarotonga (the capital) by even greater distances (several days boat journey). Puka-Puka has reportedly not changed considerably from Frisbie's time, but the other atolls have developed considerably because of local pearl industries. They are also reported to be less egalitarian than in Puka-Puka. New Zealand is a major aid benefactor of the Cook Islands. The Cook Islands are independent, but the atoll dwellers must compete with the Southern Cooks for their share of the funding. The aid, labor privileges, and emigration opportunities are expected to continue into the foreseeable future. There is considerable migration to both Rarotonga and New Zealand which has led to a negative population growth rate in the Cook Islands.

The Tuamotu Archipelago is the easternmost group of atolls in the Pacific and the largest assemblage of atolls in the world. It is administered by France as part of French Polynesia. It is subject to frequent devastation by hurricanes, which may have led to the decline in root crop production during the copra era. The atolls were frequently visited by missionaries and traders, and traditional culture is not as strong as in the other groups. The French Government has taken steps to promote development in the atolls. Employment has also been generated by the introduction of tourism and military bases. A number of innovative research projects are under way on the atolls including irrigated horticulture and alternative energy sources. There is considerable emigration to Papeete, the capital of Tahiti. There is, if anything, a problem of negative population pressure on most atolls.

The Federated States of Micronesia is an extended group of atolls, raised atolls, mixed atolls, and high islands spanning a great distance across the Northwestern Pacific, and is frequently visited by hurricanes. Formerly a U.S. territory, it became independent recently and is now in a Compact of Free Association with the U.S. The four states of Truk, Ponape, Kosrae, and Yap are each administered from a central high island but only the atolls are considered here. There is extensive reliance on U.S. aid. The atolls are still traditional but material aspirations are gradually

increasing. Atoll residents have reportedly had little input into the planning process (Kent, 1982) and there is also inappropriate delivery of western style health and education services (Robillard, 1984). These difficulties are compounded by different languages and cultures and little essential unity. There is considerable migration to high islands, but the status of these atoll minorities is very low compared to the situation in Rarotonga and Papeete, and is related to cultural factors including poor communication, rigid hierarchies, and caste differentiation (personal communication, B. Robillard and B. Raynor). Population levels are stable in Ponape and Yap but they are increasing in Truk (possibly due to limited employment in the already overpopulated district center).

Independent Groups

The independent atoll groups include (in order of increasing population size) Tuvalu, the Marshall Islands, Kiribati, and the Maldive Islands. The Maldives are by far the most populous atoll group and comprise the only major atoll group outside of the Pacific. However, as in the Tuamotus, the population density is partially alleviated because of the large land area. Large urban populations are present in the Marshalls, Kiribati, and the Maldives (table 1). Population growth is increasing dramatically in every one of these groups (table 2). Although rates of increase are similar, the absolute population growth is largest in the Maldives because of the large standing population. If present trends continue, extrapolation of present growth rates would predict dramatic increases in the populations of all of these groups by the turn of the century.

Tuvalu is a group of eight medium sized atolls with adequate rainfall not far from Tokelau. It is fortunate in that (like in Tokelau) its community cohesion is generally very strong and its sharing ethic buffers the vagaries of nature and the world economy (see Chambers, 1982). It has the smallest (and youngest) urban center but it is already beginning to manifest some of the considerable problems that plague Majuro, Kwajalein, and Male including crowding and the creation of an urban elite (personal communication, numerous travellers). Because of the small size of the atolls, there is a high population density. In the past, employment in Nauru and Tarawa provided an important source of remittance and relief of population pressure. However, as Tuvalu became separated from Kiribati, and as the phosphate reserves dry up, these limited opportunities dry up while the population in Funafuti expands. There has been a small trickle of migration to neighboring islands (from Funafuti), and while family planning programs are being advocated by the administration, population continues to climb.

Kiribati comprises three major atoll groups including Kiribati proper, the Line Islands, and the Phoenix Islands. It spans an enormous distance across the Pacific. All of these groups are subject to severe droughts. Kiribati has the largest atoll population in the Pacific. Its capital, Tarawa, is also the largest urban center in the Pacific atoll groups. It has been affected by crime, water pollution, water supply problems, unemployment, and malnutrition. Urban political power has increased "under the weight of sheer numbers and militant, urban based labor unions" (see Connell, 1983). Kiribati is attempting to cope with these problems by initiating a number of research and development projects including aquaculture, commercial fisheries, a maritime training school, and encouragement of cottage industries. The indigenous culture has traditionally been favorable to commercial enterprise. However, overseas migration and employment opportunities are extremely limited and Kiribatians are reluctant to migrate to the drought prone atolls in the Line and Phoenix Islands. To cope with rising population pressure, a family planning program has been initiated (Macrae, 1983).

The Marshall Islands are composed of two atoll chains running in a north-south direction at the eastern fringe of Micronesia. Kiribati is the nearest neighbor. Periodic drought poses natural limitations which severely restrict the potential for further population growth. It has the highest growth rate in the Pacific and the largest percentage of urban population (sixty-three percent in 1980). These data may be related to migration from northern atolls because of droughts and radioactive contamination from U.S. nuclear tests in the 1950s. This has, in turn, led to the worst urbanization problems in the Pacific including the emergence of gangs, drunkenness, fights, malnutrition, lagoon pollution, and recurrent epidemics; prompting the administration to initiate an "operation exodus." Marshallese have the option of employment in the U.S. but few have taken advantage of this opportunity.

The Maldive Islands are the only major group of atolls in the Indian Ocean and are culturally [quite] distinct from the Pacific atolls. A comprehensive socioeconomic survey was recently conducted (World Bank, 1980). The summary below relies on this report, supplemented by personal communication (A. White): The Maldives are a group of about twenty large, inhabited atolls closest to India and Sri Lanka. They are the most populous group of atolls in the world and are notable for the pervasive influence of a cash economy even on the outer atolls. The society is hierarchically organized into classes. There is presently severe maldistribution of resources, as mentioned above.

Outer atoll administrators are usually persons from the capital. Even the fisheries profits on outer atolls mainly accrues to a few boat owners. Land is leased to developers for private enterprise who have little interest in long term conservation. Consequently, the natural forest has largely been stripped to a virtual desert environment, the reef coral is excavated for construction, and consumption is based largely on imported food. Similarly, profits accruing from tourism are poorly distributed. In contrast to Pacific atolls, there is a low life expectancy, leprosy, tuberculosis, malaria, and widespread malnutrition. Health facilities are meager and education is provided mainly by Koranic schools. In spite of the rapid growth rates, the culture is adverse to family planning.

SUMMARY

Populations in the Tokelau Islands, the Northern Cook Islands, the Tuamotu Archipelago, and the outer islands in the Federated States of Micronesia are characterized by low growth rates, continuing migration, and minimal urbanization. In some areas, there is a concern with excessive depopulation to high islands and the mainland. In contrast to these areas, on Tuvalu, Kiribati, the Marshall Islands, and the Maldive Islands, there is concern about population pressure in district centers due to high birth rates, and limited opportunities for migration. Crowding in district centers has led to pollution, recurrent epidemics, malnutrition, crime, social disintegration, and foreign dependence; and there are concerns that standards of living will further decline.

CARRYING CAPACITY

Traditional Models

Carrying capacity is defined as the maximal population supportable in a given area. Biologists often use the term to refer to the amount of plant and animal biomass that can be sustained on land or in the water. Carrying capacity has been used more specifically by social scientists in reference to human populations. The problem of feeding growing populations with limited resources was enunciated clearly by Malthus in 1801 (Malthus, 1929), who postulated,

> "First, that food is necessary to the existence of man. Secondly, that the passion between the sexes is necessary, and will remain nearly in its present state. . .Assuming then, my postulates as granted, I say, that the power of population is indefinitely greater than the power in the earth to provide

sustenance for men. Population, when unchecked, increases in a geometrical ratio. Sustenance increases only in an arithmetical ratio."

The earliest quantitative model for carrying capacity is the logistic equation, developed independently by Verhulst (1838) and Pearl and Reed (1920). The key parameters are the rate of natural increase and the maximal carrying capacity. The variable is the number of persons in the population. The result is a sigmoidal curve in which the growth rate first accelerates; then decelerates. The determinants of the equation have been an issue of intense debate. Proposed mechanisms include technological, physiological, and sociological responses to increasing density. However, the logistic equation has numerous crippling assumptions such as the absence of life history characteristics, time delays, non-linear effects, and differences among segments of the population (Wilbur, 1972; Wilson and Bossert, 1971). Shifting cultivation models represent a more analytical approach and have been reviewed by Feachem (1973). Originally designed to study tropical, subsistence societies, they attempt to relate land, crop yield, and consumption in order to calculate the maximal population supportable in a unit area. They have been criticized by Street (1969) because of erroneous assumptions including constant farming technology, land-use allocation, and consumption; and losses due to pests, disease, and erosion. These models (and others) are reviewed in detail by Fearnside (1985).

Carrying capacity is particularly relevant to small islands where spatial constraints on production and population expansion can be unusually severe. In a study of the Polynesian outlier atolls in the North Solomon Islands, Bayliss-Smith (1974) relates the maximal sustainable population to land area, desired foods, net productivity, minimal consumption levels, and nutritional requirements. Although land area and per capita nutritional requirements remain fixed, the other parameters vary in response to population pressure. He attempts to avoid the shortcomings of previous models by estimating the perceived carrying capacity and by including location-specific demographic and economic factors. However, he also finds it necessary to accept several unproven assumptions including minimal influence of trade, social production, and technological advancement. A second model is provided by Bayliss-Smith (1980) in the Man and the Biosphere Project in Eastern Fiji. Adaptation and change is explicitly accounted for by a hypothesized inverse relationship (empirically validated for Pacific taro cultivation) between labor inputs and product outputs. As intensification increases, areal productivity increases but hourly productivity decreases. This increased

work load eventually requires technological innovation, fertility regulation, or migration. He provides models simulating different historical periods and allows for varied land-use allocation and technological change.

As part of the above project in Eastern Fiji, Hardaker (1980) develops an economic model using a linear programming method. It attempts to optimize productivity of an island based on various production sectors and varying land uses. He allows for variation in crop prices, quota impositions, land availability, and land redistribution. Although the model is intended for optimizing production, it could just as easily be used to optimize population or any other variable. It can thus be a used for estimation of carrying capacity.

All of the above models relate production to consumption. The more sophisticated models utilize graphics and computer programming and allow for the possibility of parameter changes. However, numerous problems remain with all of these models. Historical reconstruction is speculative; future forecasting is even more hazardous. Technological innovations may occur randomly at discreet intervals, without a uniform or predictable basis. Virtually none of the above models have been able to offer a convincing model which includes the impact of political linkages. Nevertheless; while technological and cultural changes may unpredictably affect carrying capacity in the future, there is still a need for a contemporary projection of present trends in population growth and resource availability. Urban and rural areas are increasingly being affected by fluctuations in population which affect the health of the society and the environment. Some of these events may irrevocably affect future generations, and require a contemporary consideration of carrying capacity.

The Influence of the West

In an otherwise admirable synopsis of human ecology on atolls, Alkire (1978) presents a rather simplistic typology which classifies atolls based on the degree of isolation. At the solitary extreme are atoll <u>isolates</u>, characterized by extreme isolation and restriction of the population to a single atoll. In these communities there is typically a history of overpopulation; limited agricultural intensification; resource shortages; and varying responses, including feuding, raiding, tenure alterations, fertility controls, and other demographic control measures. Coral <u>clusters</u> are an intermediate category in which two or three atolls are in close proximity to each other, and thus have greater options. In periods of population-resource

imbalance, their proximity allows economic exchange and personnel movements, including interatoll warfare and raiding. The coral complex is a third category in which the atolls are part of a complex chain of atolls, often associated with high islands. Microclimatic differences thus allowed for even greater development of a diversified, interdependent cultural system whose limits were considerably expanded.

The problem of this categorization, as Alkire himself admits, is the fact that the expansion of Western influence, along with modern transport and communications, is lessening the importance of a purely physical isolation as the significant parameter in categorizing human ecology on atolls. Beginning with the development of the copra trade by various continental powers, atolls have become more and more closely tied to world economic conditions. Extensive planting of coconut has led to a dramatic alteration of the original habitat which was formerly a complex ecosystem of unique atoll species. The copra trade initiated a period of relative affluence when islanders were able to supplement the indigenous economy with imported goods. In some areas, the exploitation of phosphates led to substantial affluence. During this period, atoll societies gradually shifted away from reliance on pit-taro, breadfruit, pandanus, coconuts, other land species, and traditional fisheries. Much of the traditional agricultural, fisheries, and navigational techniques, as well and the allied technology and social structure that had evolved to maintain this system has been lost.

Further events have also occurred which have affected atoll carrying capacity. Along with the world recession and related factors, copra prices have declined--and transport costs increased-- to the point that many atoll plantations go unharvested. Perhaps more significantly, atoll expectations in terms of living standards and social services have been raised to the point that extensive international aid has been necessary just to maintain minimal basic services. Emigration to high islands and continental powers has provided a source of remittances which provide a major source of income. These influences have locked atoll economies into a dependence system which has a depressing effect on local production since the returns cannot compare with the income provided by overseas employment or aid-sponsored wage salary. Along with the decline in subsistence horticulture, outboard motors are replacing paddles and sails, and population pyramids "resemble hourglasses" (Alkire, 1978). Moreover, local interisland transport has decreased so that some islands are more closely tied to metropolitan powers than their neighbors (Proctor, 1980).

Alkire's typology would be appropriate if atolls were to seek self reliance, return to subsistence lifestyles, and wean themselves from western aid, as advocated by Geddes, Chambers, Sewell, Lawrence, and Watters (1982) in a study of atoll economies in Kiribati and Tuvalu. Following the advice of Schumacher (1973) external development aid is compared to "a foreign body that cannot be integrated and will further exacerbate the problems." A future is envisioned in which there is revitalization of the traditional sector, import substitution, and gradual inclusion of appropriate and affordable aspects of western technology. To discourage urbanization, they recommend decentralization of government services, creation of regional substations on outer islands, elimination of town subsidies, import taxation, and financial maneuvers to discourage rural-urban migration. However, there are few atoll societies that have elected for this path. Tokelau is virtually the only atoll group that discourages both tourism and private enterprise. Yet it also relies on extensive foreign aid and migration opportunities offered by New Zealand (Rapaport, 1987). The underlying ideology that is most often heard in the islands favors a continuation of foreign aid, urbanization, and migration opportunities. It is based on the short term material advantages afforded to an educated elite residing in district centers and is supported by rural populations benefitting from modern health and education facilities.

This latter view is worded succinctly by Hau'ofa (1980), a sociologist at the University of the South Pacific (Fiji) and a native Pacific Islander: Attempting to maintain the traditional social systems would be "an exercise in futility." Given the present orientation of island governments, the best solution is to

> "do away with the preoccupation with small-scale operations and to put at least some aspects of agricultural and economic development on a large scale, high technology level. The social and cultural costs will be high but it must be made clear to the islanders that they cannot have their cake and eat it too. They cannot have the basically western lifestyle based on the high per capita GNP to which they aspire, without changing in a very fundamental way the systems of social relations and community life, all of which arose from and are therefore appropriate to subsistence existence. . . Furthermore, the smaller countries have to give up narrowly defined definitions of independence and acknowledge the likelihood of continued dependence on foreign aid because of their narrow resource base. They must expect changed life styles and, given the

> continuation of the present day opportunities for overseas migration, . . .will have to put up with continued disruptions of family life and its social implications. (Rural-urban movement) may reduce the problems of providing services to some remote rural areas. . .and the children of rural dwellers must be trained to move into non-agricultural sectors of the economy. . . .To introduce models of smallholder labor-intensive commercial agricultural development devised elsewhere for true peasant societies is tantamount to introducing a program for trapping people in rural poverty."

This is a pragmatic viewpoint that attempts to optimize the material welfare of the islanders at the cost of increased dependence on outside powers.

A Dynamic Model

The theoretical basis of the proposed model rests on the following premises: The carrying capacity of an environment may be altered due to environmental changes. Natural disasters can affect the physical shape of the land and reef as well as the allied flora and fauna. The successive stages in island colonization by living species are related to fluctuations in these conditions by the process of evolution and differentiation. Thus, the carrying capacity of an area for a biological community depends on characteristics that were derived by adaptation. Adaptive traits will cause the carrying capacity for that species to rise compared to the non-endemic species. Furthermore, carrying capacity depends on the behavior of the species. Alterations in feeding, reproductive, and other social behavior affect the amount of supportable individuals.

Human populations on small islands are affected by changes in the land, reef, and water due to both natural and social interventions. They are also affected by fluctuations in world economic conditions. Most atoll societies are linked to high islands and metropolitan powers by trade, remittances, aid, work opportunities, and migration. This

> "all affects the amount of supportable individuals on the islands. Changing perceptions of needs and standards of living are directly related to travel, modern education, and international communication. This, too, tends to modify the community requirements. In outlying areas, these expectations may cause the carrying capacity to contract. In district centers, employment, educational, and other factors may cause the carrying capacity to expand. A steady-state

> equilibrium is determined by inter-regional factors which bind outer atolls, district centers, and metropolitan powers into a single system. This model follows the suggestion of Bayliss-Smith (1980) in noting the significance of the <u>perceived</u> carrying capacity."

Carrying capacity is thus largely dependent on the expectations and the perceived needs of the population. To calculate carrying capacity based on survival alone would be useless; it would constitute an unrealistic model that ignores the desire for the quality of life. The key determinants, then, are the amount of consumption and the total resources. In a subsistence economy, the carrying capacity is determined mainly by the available food on the reefs and on land. When one of these becomes limiting, the population cannot expand further, and must either migrate, control population growth, or be curtailed through hunger or war. Contemporary atoll societies rely on a mixed subsistence and wage economy. Outer islands generally still rely heavily on subsistence production, but there is an increasing reliance of wage and aid based income. In the urbanized district centers, there is almost total reliance on income.

On the dependent atolls and on some of the independent atolls, outer island populations are static or decreasing. This indicates a contraction in the carrying capacity as perceived by outer islanders, for whom income availability, rather than food, becomes the limiting factor. Excess persons tend to migrate to the main islands. While the carrying capacity thus declines in outer islands, it expands in district centers, since imports allow the support of a greater population than allowable through indigenous food production. When the district center population demand exceeds the available support available through local jobs, the carrying capacity is perceived to be approaching its limits, and persons attempt to migrate to mainland countries. Where this option is not generally available, as in the independent groups, the available resources are no longer adequate, and the carrying capacity is overshot. Similarly, when excessive immigration to metropolitan powers becomes problematic, their own cities suffer from resource shortage. In both cases, family planning becomes imperative to avoid serious malnutrition. As the maximal carrying capacity is approached, environmental pollution and social ills becomes limiting factors.

Data have been presented which demonstrate a variety of environmental and social problems besetting overpopulated urban areas in the independent groups. These include lagoon, reef, and land pollution; violent crime; infectious

and chronic disease; mental illness; adolescent suicide; family problems; and malnutrition. These are all symptoms of carrying capacity overshoot; and are quite similar to the problems facing subsistence societies who exceeded their carrying capacity. However, the colonization and settlement of new islands is generally no longer feasible; and some of the options open to subsistence societies, such as infanticide and war, are no longer condoned. The result is a crowded district center that faces chronic population pressure, leading to gradual deterioration of both social welfare and the environment. Unlike the situation in subsistence economies, the deleterious effects of carrying capacity overshoot may be difficult to reverse, and they also result in a spillover effect to mainland immigration centers.

Philosophical Considerations

Following the contraction of the earth's frontiers and resources, and increasing maldistribution and environmental degradation, a renewed interest in Malthusian theory resulted in a Club of Rome study of the "World Problematique". This resulted in a new approach to progress which emphasized equilibrium rather than growth (Meadows, 1974). This came as a rude awakening to a society accustomed to equate growth with success. Their predictions were disputed by an English Research team at the University of Sussex (Cole, Freeman, Jahoda, and Pavitt, 1973), who argued that technological innovation and societal responses would solve the population problem without recourse to stringent growth control measures.

In a response to the Sussex team, Meadows, Meadows, Randers, and Behrens (1973) point out that a fundamental difference in the concept of man exists between the two groups. The first approach believes

> "that man is a very special creature whose unique brain gives him not only the capability but the right to exploit for his own short term purposes all other creatures and all resources the world has to offer. . .man is essentially omnipotent, he can develop at no cost a technology or a social change to overcome any obstacle, and such developments will occur instantly upon the perception of the obstacle."

The opposite concept of man is rooted more closely in Eastern traditions and assumes

> "that man is one species with all other species embedded in the intricate web of natural processes that sustains and constrains all forms of life. . .man is

> one of the more successful species, in terms of competitiveness, but his very success is leading him to destroy and simplify the natural sustaining web, about which he understands very little. . .human institutions are ponderous and short sighted, adaptive only after very long delays, and likely to attack complex issues with simplistic and self-centered solutions. . .much of human technology and `progress' has been attained only at the expense of natural beauty, human dignity, and social integrity. . .those who have suffered the greatest loss of these amenities have also had the least benefit from economic progress."

The atolls appear to be an environment in which the former perpective is extremely dangerous. Population pressure in urban centers indicate that the carrying capacity is being approached. The independent groups have felt this pressure most acutely, and have instituted appropriate family planning measures. However, a substantial lag period is expected before growth tapers, and by then population pressure will have further been exacerbated. Standards of living can be expected to decline as predicted by Alkire (1978) and Bayliss-Smith (1986). The overshoot predicted by Meadows is already being seen in these areas. The search for intensified methods of resource exploitation by development planners is risky because by attempting to remove the symptoms of impending limits, they divert attention from a pattern of growth that continues to spiral upwards. Emigration and aid can worsen the situation because, rather than addressing the issues directly, they allow a procrastination of growth control while the population continues to further expand.

SUMMARY

Carrying capacity is defined as the maximal population an environment will support. Traditional models have tended to view carrying capacity in terms of a closed system and have paid insufficient attention to political factors and contemporary demographic trends. The proposed model begins with increased expectations and perceived needs. This results in lowered carrying capacity for outlying areas, and expanded carrying capacity in district centers, leading to urbanization, emigration, and carrying capacity overshoot in both regional and mainland areas. Although it is difficult to forecast future trends, present indications of population pressure, as well as the possibility of a substantial lag period, would appear to mandate policy intervention by regional administrations and island communities.

CONCLUSION

Summarizing the above discussion, I will attempt to prioritize policy issues and highlight region-specific pressure-points by which timely and appropriate intervention could most effectively alleviate population pressure on atolls.

The natural environment is still the basis of survival on most atolls. The limited resources available should be treated with the maximum caution. Many atolls are drought prone and are likely to face serious resource shortage on a periodic basis. Indigenous varieties of trees, root crops, and other species should be carefully preserved and thoroughly investigated. Additional research is needed to identify and develop drought and salt resistant varieties. It is essential to preserve the integrity of the fresh water lens on the islets, which may be threatened by overland latrines and irrigation projects. It is also important to limit damage to the reef caused by construction, blasting, and pesticides. Subsistence production provides a long-term, ecologically secure method for survival on atolls. It is unfortunately declining throughout the Pacific in response to aid-based wages and natural disasters. Further investigation of both traditional horticulture and fisheries is needed.

At present, most atolls have very limited contact with the outside world. Regional cooperation and collaboration are hindered. Improved communications, transport, and shipping will be needed for industrial development. Tourism, export industries, pearl cultivation, and handicraft production are income generators but the shift to a money economy often yields unanticipated results. Urbanization has the ability to temporarily expand the carrying capacity of an island but eventually the carrying capacity is overshot, leading to environmental pollution, resource maldistribution, and social disintegration. The greatest problems of population pressure are currently seen on the independent atoll groups. In the dependent groups, the availability of migration and foreign support simply transfers the problem to the host countries. In most areas, an equilibrium is reached where environmental problems, scarcity of employment, social problems, and government restrictions constrain further outmigration from home areas. Anticipation of these conditions by directly addressing the population growth in home areas would strengthen local communities and alleviate spillover effects in overseas areas.

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Table 1. COMPARATIVE STATISTICS ON ATOLL GROUPS

Censuses from 1977-1983.

Source: Connell (1983); Pacific Islands Year Book (1984); World Bank (1980)

Tokelau Is.	N. Cook Is.	Tuamotu Arch.	F.S.M. Atolls	Tuvalu	Kiribati	Marshall Is.	Maldive Is.
NUMBER OF INHABITED ISLANDS							
3	6	17	29	9	20	26	20
TOTAL LAND AREA (Square miles)							
4	10	280	22	10	278	69	298
TOTAL POPULATION							
1570	2260	9800	1410	7300	59800	30900	142800
AVERAGE OUTER ATOLL POPULATION							
500	400	600	500	580	1750	460	5600
POPULATION DENSITY (Per sqm.)							
341	217	35	641	734	202	447	479
TOTAL URBAN POPULATION							
				2100	21000	18400	29500
PERCENT URBAN							
				31	32	69	21
PERCENT WAGE EMPLOYED							
12	7	20	16	12	12	13	40
DEVELOPMENT AID (Per cap. annually, $U.S.)							
1212	593	200	450	653	327	450	4851

Table 2. DEMOGRAPHIC TRENDS FOR ATOLL GROUPS

Thousands of persons

Source: Connell (1983); Pacific Islands Year Book (1984); World Bank (1980)

	1950*	1960*	1970*	1980*
TOKELAU IS.	1.3	1.8	1.6	1.6
N. COOK IS.	2.4	2.8	2.3	2.3
TUAMOTU ARCH.	8.5	9.6	8.2	9.8
F.S.M.	9.2	11.5	12.2	14.1
TUVALU	4.4	5.0	5.8	7.3
KIRIBATI		43.3	51.9	59.8
MARSHALL IS.	11.0	17.1	25.0	30.9
MALDIVE IS.			103.8	142.8

*Note: Censuses used were closest to the year indicated

ATOLL RESEARCH BULLETIN

NO. 341

MAUKE, MITIARO AND ATIU: GEOMORPHOLOGY OF MAKATEA ISLANDS IN THE SOUTHERN COOKS

BY

D. R. STODDART, C. D. WOODROFFE AND T. SPENCER

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MAUKE, MITIARO AND ATIU: GEOMORPHOLOGY OF MAKATEA ISLANDS IN THE SOUTHERN COOKS

BY

D. R. STODDART[1], C. D. WOODROFFE[2] AND T. SPENCER[3]

ABSTRACT

Mauke, Mitiaro and Atiu are deeply eroded volcanic islands in the southern Cook Islands, south Pacific, each surrounded by a rim of elevated Cenozoic reef limestone (makatea). This paper presents the results of instrumental topographic surveys of each island. The maximum elevation of the volcanics is 24.4, 8.9 and 71.0 m on Mauke, Mitiaro and Atiu, respectively, and of the makatea 14.7, 10.9 and 22.1 m. The makatea is fringed on its seaward side and in places partially overlain by a sequence of late Pleistocene reef limestones which reach maximum elevations of 12.7, 7.8 and 12.2 m respectively. These exhibit varied reef facies as well as emergent reef topographies, especially groove-and-spur systems. Elevated notches, cliff-foot benches and emergent reef flats indicate higher Holocene relative sea-levels at up to at least 3 m above present. These data are compared with similar features on Mangaia, also in the southern Cooks, and the very different topographic and stratigraphic records on Rarotonga and Aitutaki, and the implications of the independent island histories thus revealed for previous discussions of lithospheric flexure and Pleistocene sea-level change are reviewed.

INTRODUCTION

The islands of Mauke, Mitiaro and Atiu in the Southern Cook Islands rarely enter into the scientific literature. Atiu was discovered during the voyage of the *Resolution* and *Discovery* —Cook's last voyage—on 31 March 1777. Lieutenant Gore, at Cook's request, 'examined all the west side of the island without finding a place where a boat could land or the Ships could anchor, the shore being every where bounded by a steep corral rock against which the sea broke in a dreadfull surf' (Beaglehole, ed., 1967, I, 83). A landing was effected from boats at Oravaru on the west coast on 3 April, when William Anderson made the first geological and geomorphological observations:

> 'Whatever the island itself may be further in we could not tell, but towards the sea it is nothing more than a bank of coral ten or twelve feet high, steep and rugged except where there are small sandy beaches at some clefts where the ascent is graduall. The coral, though it has probably been expos'd to the

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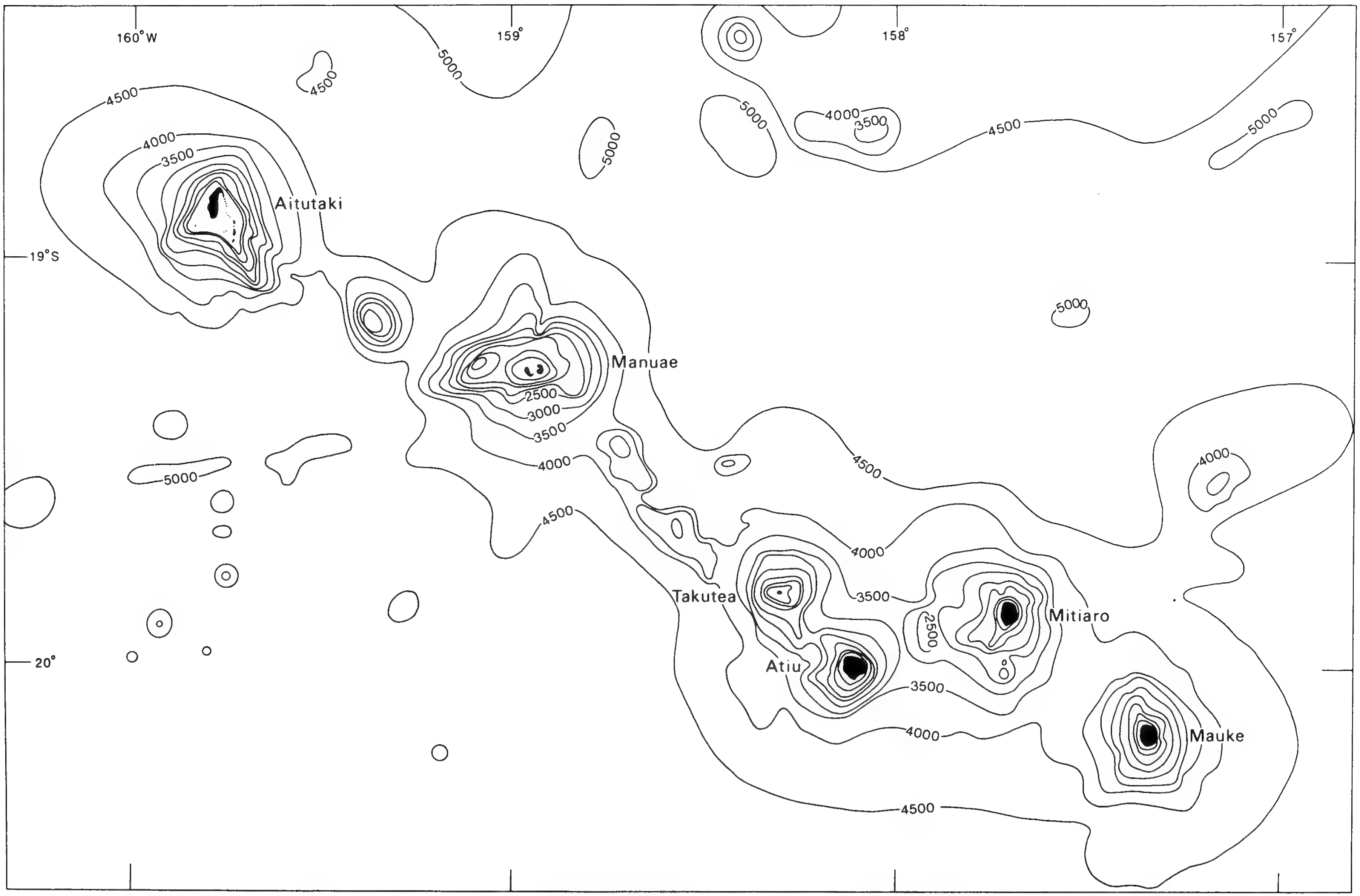


Figure 1. Bathymetry of the southern Cook Islands

> weather for centurys, has undergone no further change than becoming black on the surface, which from its irregularity makes it appear not unlike large Masses of some burnt substance; but on breaking some pieces off we found that at the depth of two or three inches it was just as fresh as the pieces that had been lately thrown on the beach by the sea. The excavations towards the sea mention'd at Mang'ya nooe nainaiwa [Mangaia] were likewise seen here, but it does not seem that they are the effects of the waves dashing violently against the shore; for it is entirely lin'd by a reef or rock running to different breadths into the sea, where it ends all at once and becomes like a high steep wall. It is nearly even with the surface of the water & of a brown or brick colour, but the texture is rather porous though sufficient to withstand the washing of the surf which breaks continually upon it. The soil where we were is light & sandy but within it may differ, as we saw from the ship a reddish cast upon the rising grounds as at Mang'ya ...' (Beaglehole, ed., 1967, III, 841-842).

But Cook stood off for Takutea the following day and the observations were not pursued. Anderson's may be the first description in the literature of an algal ridge, as well as of cyanobacterial darkening of reef limestones.

John Williams called at Mauke and Mitiaro as well as Atiu fortyfive years later, during his missionary voyages in 1822, when he described the karst caves for the first time (Williams 1838). Others, including Byron in H.M.S. *Blonde* and W. W. Gill, visited the islands later in the century, but added little of geomorphological significance.

The geology of Atiu was the subject of a report by Marshall in 1930 during the New Zealand geologist's more substantial investigations of Mangaia (1927) and Rarotonga (1930). Marshall and his contemporaries (e.g. Chubb 1927a) realized that the distinctive island types found in the southern Cook and Austral Islands in the central South Pacific posed particular problems of interpretation, with important consequences for the theory of coral reef development, island evolution, and sea level change. These islands, notably Mangaia, Mauke, Mitiaro and Atiu in the Cooks, and Rurutu and Rimatara in the Australs, consist of eroded volcanoes of Cenozoic age, wholly or partially surrounded by uplifted, karst-eroded Cenozoic reef limestones (*makatea* in local usage). Between the central volcanics and the often vertical inner walls of the makatea there is frequently a depression close to sea-level, with swamps, occasional streams, and standing water.

Marshall (1927, 1929) believed that these features represented an uplifted barrier reef and former lagoon surrounding the volcanic island. Chubb (1927b) and Hoffmeister (1930) believed the depression between volcanics and makatea to be of solutional origin and the gross topography of these islands to be therefore secondary. In our previous studies of Mangaia (Stoddart et al. 1985) and Rurutu (Stoddart and Spencer 1987) we have shown that in these two cases the second of these views is correct.

Nevertheless, two interesting questions remain. The first concerns the degree of uplift of the islands as shown by the maximum elevation of the makatea. This varies from ca 10 m on Mitiaro and Rimatara to 73 m on Mangaia and 100 m on Rurutu. McNutt and Menard (1978) in a remarkable pioneering paper hypothesized that uplift resulted from crustal loading through the formation of nearby younger volcanoes and consequent elastic deformation of the crust. Thus the formation of Rarotonga in the Pleistocene could account for the elevation of islands in the southern Cooks such as Mangaia and Atiu, and of Tahiti the elevation of Makatea; they gave many more examples. The degree of uplift in each case would be a function of distance from the load and the magnitude of the lithospheric flexure. Calculations of uplift by McNutt and Menard (1978) and others (e.g. Lambeck 1981a,

1981b) showed apparently close relationships between theoretical predictions and actual island topography, though in the case of many islands the elevations of both volcanics and makatea were in fact very inadequately known (Spencer et al. 1987). The more precise determination of the altitudes of geomorphic features on these islands thus has important consequences for the interpretation of island development and crustal behaviour in the Pacific.

Second, and particularly after the classic paper by Veeh (1966), it was realized that Pleistocene fluctuations of sea level must have had stratigraphic and geomorphic consequences on these emergent islands, and that these fluctuations could be calibrated using radiometric dating techniques. Many workers, especially in the southern Cooks, had already drawn attention to the presence of more or less well-marked terraces and notches apparently indicative of high sea level stands (Grange and Fox 1955, Schofield 1967, Wood and Hay 1967, Campbell 1982), but the elevations, extent and significance of many of the features to which they drew attention were only weakly established. In our earlier work on Mangaia we identified reef deposits and geomorphic features related to a sea level of last interglacial age (and perhaps earlier) (Stoddart et al. 1985) and calibrated these with uranium series ages (Spencer et al. 1988).

The present study concerns three further islands in the southern Cooks. Mauke, Mitiaro and Atiu were visited by us in June 1985. All three authors were responsible for the surveys on the first two islands. Woodroffe was primarily responsible for the surveys on Atiu, though Stoddart and Spencer also visited the island and inspected the profile sites. The aim of this paper is to present a detailed descriptive geomorphology of each of these islands, with particular reference to the limestones, derived from instrumental levelling of profiles transverse to the coasts. We have determined the elevations of both volcanics and makatea on Mauke and Mitiaro, though on the larger islands of Atiu our surveys were limited to coastal sequences. On all three islands we have found diverse evidence, both morphological and stratigraphic, of late Pleistocene sea level fluctuations. Sequences of radiocarbon and uranium-series dates for Holocene and Pleistocene deposits are available and will be reported elsewhere (Woodroffe *et al.*, in press; Woodroffe *et al.*, in preparation), but they confirm the complexity of the record established in the field and also show that the features we describe are not confined in age to Last Interglacial times.

STUDY AREA

Geomorphology

The southern Cook and Austral Islands comprise two parallel chains of islands extending over some 22° of longitude or ca 2600 km. The southernmost extends from Macdonald Seamount in the southeast to Rarotonga in the northwest, and the northernmost from Rapa and Marotiri in the southeast to Palmerston in the northwest. The existence of these clear linearities, however, disguises the complexity of geomorphic evolution within and between them, and it is clear both from the geomorphic features of the islands themselves and our knowledge of the age of volcanism at each (Jarrard and Clague 1977) that the chains have not developed in simple linear manner from a fixed hotspot (as, for example, the Hawaiian Islands), in which island age and degree of geomorphic development are a simple linear function of distance from the hotspot.

In the southern Cooks, especially, only the volcanics of Mangaia fit the model of age and distance predictions from the Macdonald hotspot: Mauke, Mitiaro and Atiu, as well as Aitutaki and Rarotonga, are all substantially too young. Indeed it has been

commented that in spite of such clear island-chain linearity, 'the Austral-Cook chain is clearly the least convincing example of age-distance correlation' among the island chains of the Pacific (Okal and Batiza 1987, 4). Furthermore, the recent detection of ten uncharted or mislocated seamounts in this region reinforces the impression of a complex geological history for the archipelago (Lambeck and Coleman 1982, Diament and Baudry 1987, Baudry et al. 1987, 1988).

The islands studied here comprise a sector of the northern chain extending between Mauke and Aitutaki, contiguous at the 4.5 km isobath (figure 1). Of the six islands in this group Aitutaki is an almost-atoll with a substantial residual volcano 124 m high, but with no elevated Pleistocene or Holocene reef limestones (Stoddart 1975); Manuae and Takutea are reefs and reef islands close to present sea level (though there is no recent account of either, other than Summerhayes's (1971) on the sediments of Manuae) and we rely for most of our information on their geomorphology on the reports of Cook's second voyage in 1777); and Atiu, Mitiaro and Mauke are makatea-encircled volcanic islands, with the components of central volcanics, makatea and swamps, though of very different individual characteristics.

K-Ar dates of volcanics give ages in excess of 8.1 Ma for Aitutaki, though with renewed volcanism at 0.7-1.9 Ma. Atiu volcanics, reaching 72 m above sea level, date at 8-10 Ma; Mitiaro volcanics, reaching 8.9 m, date in excess of 12.3 Ma; and Mauke volcanics, reaching 24.4 m, are in excess of 6.0 Ma (Jarrard and Clague 1977). The three western volcanic islands lack elevated limestones, whereas on Atiu, Mauke and Mitiaro the makatea reaches elevations of 22.1, 14.7 and 10.9 m, respectively (data from this survey). We will also show in this paper that there is evidence of late Pleistocene sea levels up to 12.2 m on Atiu, 10.0 m on Mauke, and 9.8 m on Mitiaro.

Climate

All these islands lie in the Southeast Trades and have tropical climates (see Thompson 1986, from which this summary is mainly derived). Mean annual temperatures are in the range 24-26°C with absolute extremes at Mauke over the period of record (1968-1988) of 34.8°C (in October) and 13.1°C (in July). Seasonality is determined by the latitudinal shift of the South Pacific Convergence Zone, which forms the boundary between the equatorial easterlies and the Southeast Trades. This boundary moves south over the islands, giving wet weather (yielding two-thirds of the annual precipitation) during November to April, and retreats north, giving dry weather during the Trades, from May to October (Table 1).

Table 1. Rainfall of Mauke, Mitiaro and Atiu

	Mean annual rainfall, mm	Wet season rainfall Mean, mm	Wet season rainfall %	Dry season rainfall Mean, mm	Dry season rainfall %
Mauke	1773	1156	65	617	35
Mitiaro	1826	1185	65	641	35
Atiu	1970	1336	68	634	32

Source: Thompson (1986, 29, and personal communication)

At Mauke during 1967-1971 easterlies and southeasterlies occurred 58% of the time (the Trades), and winds from the northwest, north and northeast 24% of the time (the wet season). On the same island mean monthly wind speeds averaged 3.1 m/sec during February-April, and 4.1 m/sec during August-November. The annual average of 3.6 m/sec compares with 6.7 m/sec over the adjacent open ocean, though island figures are much affected by aspect and topography.

Mean annual rainfalls are 1773 mm at Mauke (1929-1987), 1828 mm at Mitiaro, and 1970 mm at Atiu (records since 1958). These figures are subject to local topographic control on each island, though this effect is likely to be least on Mitiaro. Inter-annual variability in rainfall is considerable, both in annual and in monthly totals. Table 2 gives mean and extreme figures for the islands. The greatest monthly range at Mauke is between 689 and 5 mm in the month of November, at Mitiaro between 931 and 3 mm in the month of June, and at Atiu between 752 and 0 mm in the month of May. To some extent this variability is explained by irregular movements of the South Pacific Convergence Zone, which themselves correlate with the Southern Oscillation (the longitudinal variation in atmospheric pressure between east and west tropical Pacific). When the SPCZ is unusually far north, rainfall in the southern Cooks may be only 30-40% of the mean.

Hurricanes, defined as low-pressure circular storms with winds in excess of 32 m/sec, are common in this sector of the Pacific and are often of great violence; for a catalogue of more extreme storms in the southern Cooks, see Stoddart (1975, 8). Since 1969, when satellite surveillance began, hurricane frequency has averaged 1.4 per annum in the area.

METHODS

Elevations were determined using a Kern automatic level. The tidal range on these islands has not been established, but it is probably about 80 cm. Because of exposure of the shorelines and rough state of the sea an acceptable survey datum can only be established at low water. We attempted where possible to use the ordinary crest of the algal ridge at the reef edge as the datum for the profile surveys. This usually coincides with the tops of living microatolls in reef flat pools, and also with the lower limit of sand in coastal pocket beaches. Where the algal ridge was inaccessible because of sea conditions, the lower limit

Table 2. Monthly mean and extreme rainfalls (mm) at Mauke, Mitiaro and Atiu

MAUKE (1929-1987)													
Monthly mean	203	226	199	146	151	84	79	100	93	110	166	216	1773
Absolute maximum	549	570	594	415	499	243	269	414	341	380	689	581	3294
Absolute minimum	9	11	1	4	3	6	0	2	3	4	5	7	150
MITIARO (1959-1982)													
Monthly mean	273	204	196	183	138	130	83	88	115	89	149	180	1828
Absolute maximum	554	403	473	495	550	931	201	288	303	201	280	418	2770
Absolute minimum	72	46	0	21	6	3	7	14	19	10	19	9	1079
Mean number raindays	10	9	7	7	5	5	5	5	6	5	8	5	77
ATIU (1959-1982)													
Monthly mean	209	229	223	206	177	84	81	101	81	110	162	307	1970
Absolute maximum	490	732	525	396	752	210	227	488	251	471	479	621	3746
Absolute minimum	5	49	65	7	0	9	0	0	0	0	33	0	690
Mean number raindays	7	9	9	9	6	5	4	3	4	5	6	7	74

Source: Thompson (1986, 30, and personal communication)

of sand, which is sharply defined, was used to establish a datum. This datum approximates mean low water, as we have established by precise levelling to benchmarks during earlier work at Rarotonga. Yonekura et al. (1986, 52; 1988) also use the tops of reef flat microatolls as their datum for surveys on Mangaia, and they too believe that this approximates mean low water. In our earlier surveys at Mangaia we used the same algal ridge datum as in this paper (Stoddart et al. 1985). On Mauke we established a benchmark on the base of the white monument at Taunganui (corner nearest the Meteorological Station), at 8.11 m. A second benchmark at 23.55 m was established at the end of profile F, on the metal grid supporting two water tanks adjacent to the pumping shed. On Mitiaro a benchmark was established at 8.73 m at the foot of the water tank steps adjacent to the Cook Islands Christian Church at Mangarei. These benchmarks were used to coordinate the trans-island profiles, and can be redetermined whenever tidal records become available at Mauke and Mitiaro. At Atiu all except E and F of the surveyed profiles were independently calibrated, and no single island datum therefore exists. A level of 10.09 m above mean sea level was determined on the concrete base of the main shed at Taunganui Landing, and elevations on profiles E and F relate to this. Datums of mean sea level on other Atiu profiles were derived from still-water levels and the tidal predictions for Rarotonga (assuming the latter to be lagged two hours relative to Atiu). The datums so established are generally less than 10 cm different from an algal ridge datum.

MAUKE

The island of Mauke (figures 2 and 3) is located in latitude 20°08'S., 157°21'W., 190 km northeast of Rarotonga. It forms the summit of a 4 km high conical volcano that is approximately 35 km in diameter at its base (Summerhayes and Kibblewhite 1969). The island itself has maximum dimensions of 6.4 km N-S and 4 km E-W. Previous workers cite the total area as 18.4 sq km or equivalent (Grange and Fox 1955, 22; Wood and Hay 1970, 36; Wilson 1982, 7). Planimetry of the 1:12,500 topographic map produced photogrammetrically by the New Zealand Department of Lands and Survey (1975) yields an area of 20.3 sq km, of which 5.4 sq km represents the central volcanic area and 14.9 sq km peripheral limestones. Valley-floor swamplands on the volcanics and between the volcanics and the limestones are smaller than on other similar islands in the southern Cooks. Similarly, the makatea cliff topography at the seaward margin of the swamp areas is subdued. This cliff is generally only 4-5 m high and only locally reaches 7-8 m, and exceptionally 10 m, in height.

Volcanics

The central volcanics form a bevelled plateau at heights variously estimated at ca 100 ft [30 m] (Grange and Fox 1953, 22), 30 m (Schofield 1967, 119), 27 m (Wood and Hay 1970, 36), and 25-30 m (Wilson 1982, 9). The 1:12,500 topographic map shows spot heights on the plateau of 22-28 m, with valley floors descending to 2-12 m above sea level. Our levelling in 1985 yielded a maximum elevation of 24.4 m on profile BD (figure 4), with other peaks on the same profile of 23.0 and 23.9 m. The greatest elevation on profile BF is 23.6 m. Valley floor marsh levels in profile BF stand at 5.3 and 9.2 m.

Note that in modelling the uplift of Mauke, McNutt and Menard (1978, 1208) assumed a maximum elevation of 30.0 m and calculated uplift at 28.8 m; and Lambeck a maximum elevation of 30 m.

No volcanic bedrock is exposed on Mauke: the slopes are covered by deep brown and red soils described by Wilson (1982). Turner and Jarrard (1982, 193) give 11 K-Ar dates on olivine basalt cobbles from three localities, ranging from 4.64±0.14 to 6.30±0.20 million years. They quote (1982, 203) a weighted mean of six samples of 5.99±0.19 million years. These ages must be considered minimal estimates because of weathering.

Limestones: makatea

The makatea peripheral to the volcanics forms a zone 0.8-1.6 km wide. It consists mainly of presumably Cenozoic limestones, with a narrow seaward fringe of late Pleistocene reef limestones: the difference between these formations and the stratigraphic variability within the Pleistocene limestones have not been previously recognised. The elevation of the makatea has been variously estimated. Grange and Fox (1953, 22) give a height range for the upper surface of 30-70 ft [9.1-21.3 m], and comment that 'the makatea differs from most others [in the southern Cooks] in that the surface deposit is not a red heavy volcanic soil, this no doubt being due to the fact that the uplift of the makatea is of more recent date'. Schofield (1967, 119) quotes elevations for the outer makatea of about 9 m and for the inner makatea 21 m. Wood and Hay (1970, 36) give a maximum elevation for the makatea of 18 m, and refer to 'vague benches' at 4.6 and 12 m. Wilson (1982, 9) gives a height range of 5 to 12-15 m and notes that 'large ... pinnacles are absent'. The 1:12,500 topographic map gives spot elevations on the makatea of 6-19 m.

The greatest elevation found in our profiling was 14.65 m in profile BD, followed by 14.6 m in AB, 13.1 m in BC, and 12.2 m in J (Figures 4 and 6). The maximum makatea elevations in other profiles were between 8.4 and 9.7 m. It is possible that previous height estimates have been exaggerated, though there are many areas we did not penetrate. The contact between the inner edge of the makatea and the underlying volcanics was determined in four profiles, at 8.3 m in E, at 10.4 m with an isolated block of makatea at 11.8 m in BC, at 11.95 m in AB, and at 10.8 m in BD.

Limestones: Pleistocene

Pleistocene reef limestones form a narrow zone round the shores of the island. They are identified and distinguished from the makatea limestones by their abundant corals, especially massive *Porites*; by subhorizontal stratigraphic discontinuities (termed by us 'contacts') of the kind we have previously described at Mangaia (Stoddart et al. 1985, 134), though apparently without terrestrial paleosols; and by characteristic topographic features such as grooves, residual pillars, and horizontal notches indicative of former sea levels. Unfortunately the contact between the Pleistocene limestones and the makatea against which they have been deposited is generally mantled by recent perched beach deposits and hence the Pleistocene unit cannot readily be precisely defined. We believe that the complex of depositional and erosional features identified in these limestones represents a sequence of events during the later Pleistocene, and this is confirmed by the wide range of four uranium age determinations now available and which are reported elsewhere (Woodroffe et al. in preparation). The understanding of the unit is made problematic by the way in which depositional sequences are controlled by pre-existing erosional topography and are in their turn erosionally modified and overlapped by later deposits. Many of the topographic features on these limestones we believe to be of marine origin (horizontal notches indicative of intertidal processes; transverse grooves derived from former groove-and-spur formation, possibly with subsequent karst modification); others may be subaerial karst features.

Maximum elevations on surfaces interpreted at Pleistocene are generally 8-10 m (9.45 m on profile A, 8.11 m on B, 8.67 m on C, 10.03 m on D, 9.6 m on E, 9.41 m on G, 8.50 m on J), with a minimum of 5.97 m on H and a maximum of 12.71 m on F. The elevation of the outermost makatea on each profile (in most cases where it passes beneath the perched beach) is at equivalent elevations or slightly lower: 7.63 m on profile A, 7.61 m on B, 7.98 m on C, 9.39 m on D, 10.78 m on F, 8.91 m on G, 8.97 m on H, 11.89 m on J, and 8.48 m on L (Figures 4-6). Leaving aside the anomalously high elevation on profile J, these figures suggest an upper limit for late Pleistocene reef limestone deposition of ca 10 m. A sea level at this height would have inundated much of the lower makatea, and it is possible that marine erosion at and near this elevation accounts for the extensive areas of makatea at 8-10 m. Under such conditions the higher parts of the makatea would have formed low islands rising 2-5 m above this high sea level. The probability of the deposition of thin, patchy but laterally extensive Pleistocene reef limestones on shallowly submerged flat-lying makatea surfaces increases the difficulty of readily distinguishing units in the field.

Cliff sections in the unit here identified as Pleistocene frequently show a basal discontinuity. Where measured this stands at 1.5-2.75 m above present sea level. It is variable in elevation both laterally and transversely. In profile B it varies in elevation northwards from 1.8 to 2.1 m and southwards from 2.2 to 2.4 m. At C it stands at 2.7 m, at J at 1.5 m, and at L at 2.75 m. The surface of the underlying unit at this discontinuity is smooth rather than pinnacled.

Coastal morphology

There is a continuous reef flat around the island. It has an average width of 150-160 m, reaches a maximum of 190 m, and is only 75-110 m wide along the northeast coast between Angataura and Uriaata: the flat is thus the narrowest in the southern Cooks. It terminates landward in a cliff, usually notched, with occasional pocket beaches. The seaward edge of the flat is rimmed by an algal ridge, the presence of which means that there are no surf benches at the cliff itself.

Intertidal notches are characteristically 4-5 m in horizontal extent; the largest measured was 7 m deep in profile D. The elevation of the deepest part of the notch varies from 0.6 m (profile A) to 1.5 m (profile F). The height of the visor is more variable, doubtless in response to differences in exposure, ranging from 0.9 m (profile D) to 5.7 m (profile E). At any given locality the visor may be a double or even multiple feature. For example there are pronounced levels at 2.6 and 5.7 m near profile E and at 0.9, 1.4, 3.5 and 4.4 m near profile D.

In places where the notch does not exist there are indications of a terrace or bench at the foot of the cliff. This spur-end bench is best developed at Anaraura, south of profile C, where it is a conspicuous feature at an elevation of 2.7 m.

Deep narrow transverse grooves intersect the cliffs around the entire coastline of the island (figures 7 and 8). These resemble the grooves near Oneroa on Mangaia which we have interpreted as elevated fossil groove-and-spur features (Stoddart et al. 1985, 134). A sample groove on profile A is 3-4 m wide, and its floor rises from 3.8 to 7.0 m over a distance of 32 m. Floors of grooves have been measured at elevations of up to 7.5 m (profile D).

In the northwestern part of the island, south of Taunganui, the cliff line is conspicuously castellated, with limestone towers rising above the general level near the

crest line. The base of these towers (profile L) stands at 4.6-4.7 m. Each is surrounded by a discontinuous notch with its floor at 5.5-6.5 m. In one case the deepest part of the notch stands at an elevation of 6.7 m and the visor at 7.3 m. The irregularly eroded summits of the towers reach elevations of 8.1-8.59 m. Seaward, on this profile, there are well developed transverse grooves with floors at up to 3 m above sea level.

Holocene coastal features

Perched beaches in the form of wide expanses of cover sands overlying the limestones are found around the coast at distances of 50-150 m from the cliff top; the mean distance in the profiles measured is 85 m. Interpreted as contemporary storm deposits, these perched beaches are 50-150 m wide (mean 90 m), and their inner edges lie at 125-230 m (mean 175 m) from the cliff edge. Maximum elevations on the sand surface range from 9.1 m (profile C) to 12.7 m (profile F). These perched beaches have not been trenched, but are presumably no more than 1-2 m thick at a maximum. As noted above, they effectively mask the contact between the Cenozoic makatea and the Pleistocene limestones.

Massive perched boulders on the surface of the limestones inland from the cliff edge are common close to the shore. On profile A there are two, 1.8 and 1.4 m in height respectively, standing at elevations of 9.2 and 8.7 m above sea level, at distances of 170 and 200 m from the cliff edge (figure 10). On profile C there are three, with dimensions of 3.5x2.0x1.2, 2.8x2.6x1.2, and 5.4x2.3x1.5 m, and volumes of 8-15 m^3, at an elevation of 6.9 m above sea level, and 75 m inland from the shore. Another on profile J is 1.1 m high and stands 11.5 m from the sea. We have no data on the age of these boulders, but they are not conspicuously eroded and none of them stands on erosional pedestals. They have presumably been entrained and carried inland by storm waves during hurricanes or other extreme events: Moore and Moore (1984) have recorded boulders of coral up to 1 m in maximum dimension at elevations up to 326 m on Lanai, Hawaii, which they suggest were deposited by giant waves generated by submarine landslides. Blocks up to 6 m high on the reef flat at Rangiroa Atoll, Tuamotus, described by Stoddart (1969), have been ascribed by him to hurricanes, and by Bourrouilh-Le Jan and Talandier (1985) to either hurricanes or tsunamis. The extreme hurricanes of 1903, 1905 and 1906 are known to have deposited storm blocks at Rangiroa and Raroia of the same magnitude as those on Mauke, though at sea level rather than on cliff tops (Bourrouilh-Le Jan 1985, 315).

Blocks formed by cliff collapse consequent on intertidal undercutting are also common on the inner part of the reef flat adjacent to the cliffs (figure 11). Frequently these can be related to cliff-face scars whence they originated.

Pocket beaches of carbonate sands occur at intervals around the island. In some places beachrock formed on these beaches appears to stand at anomalously high levels. The highest elevation measured on beachrock was 1.96 m on profile F.

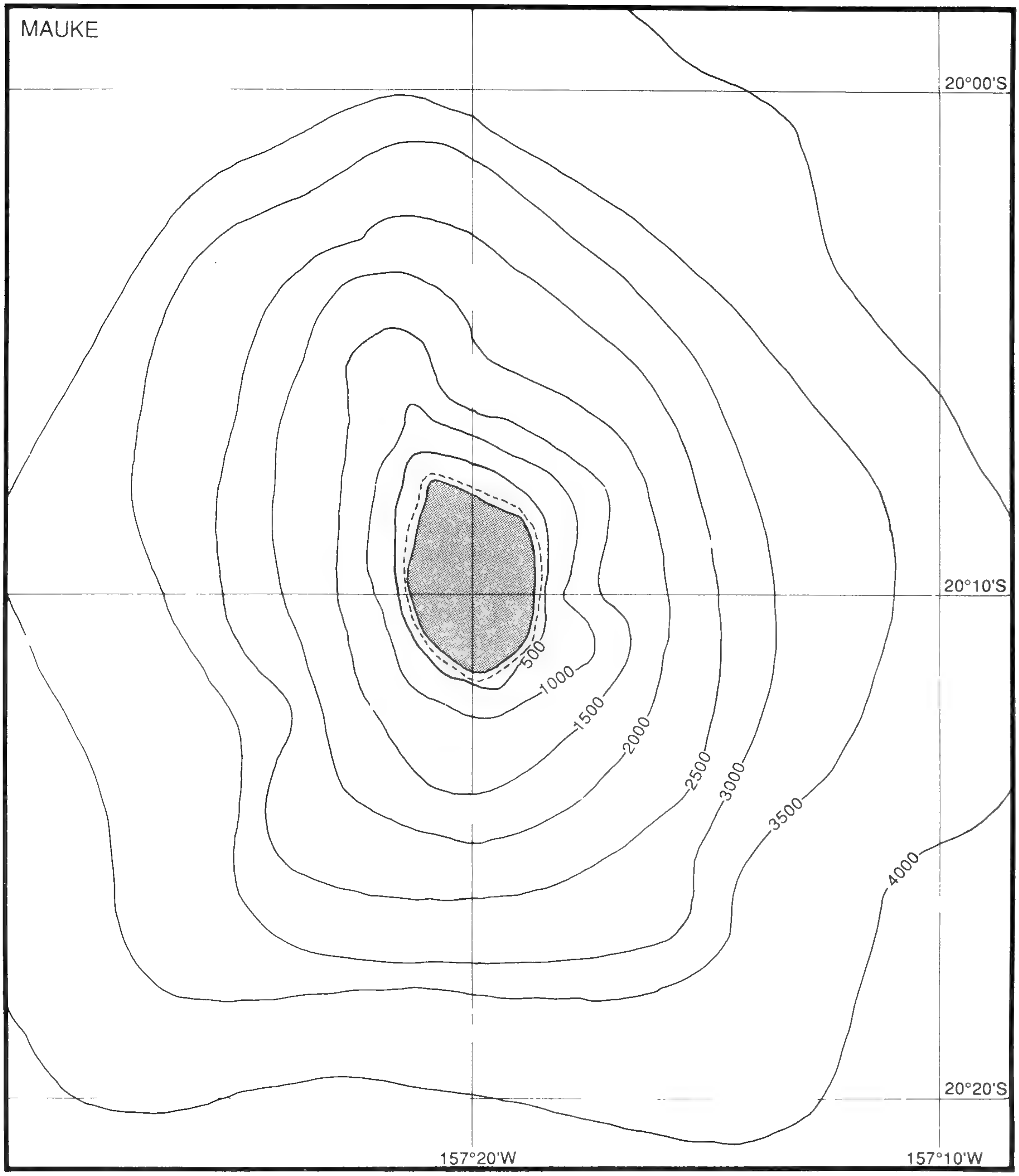


Figure 2. Bathymetry of Mauke (after Summerhayes and Kibblewhite 1969)

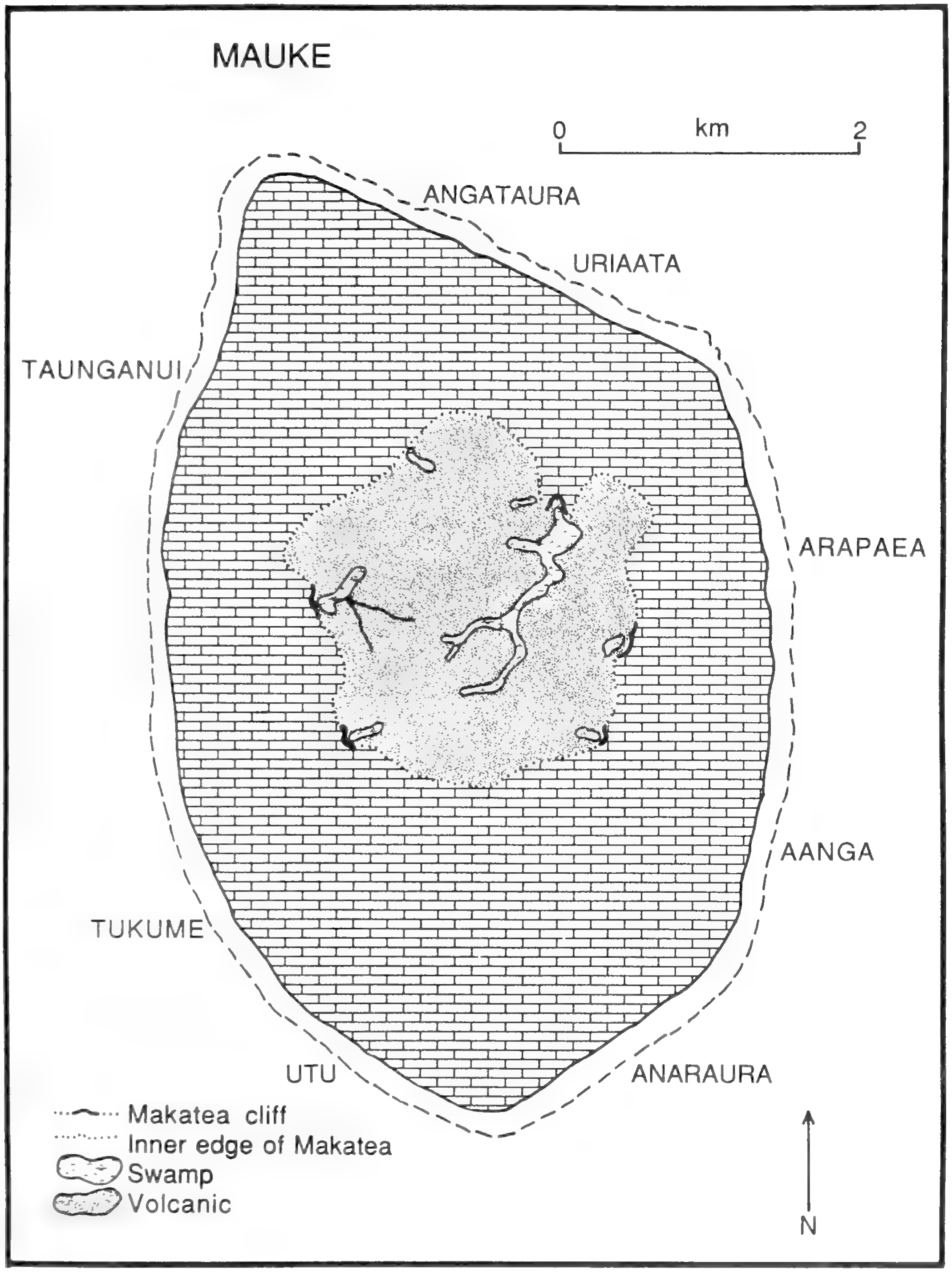


Figure 3. Geology of Mauke

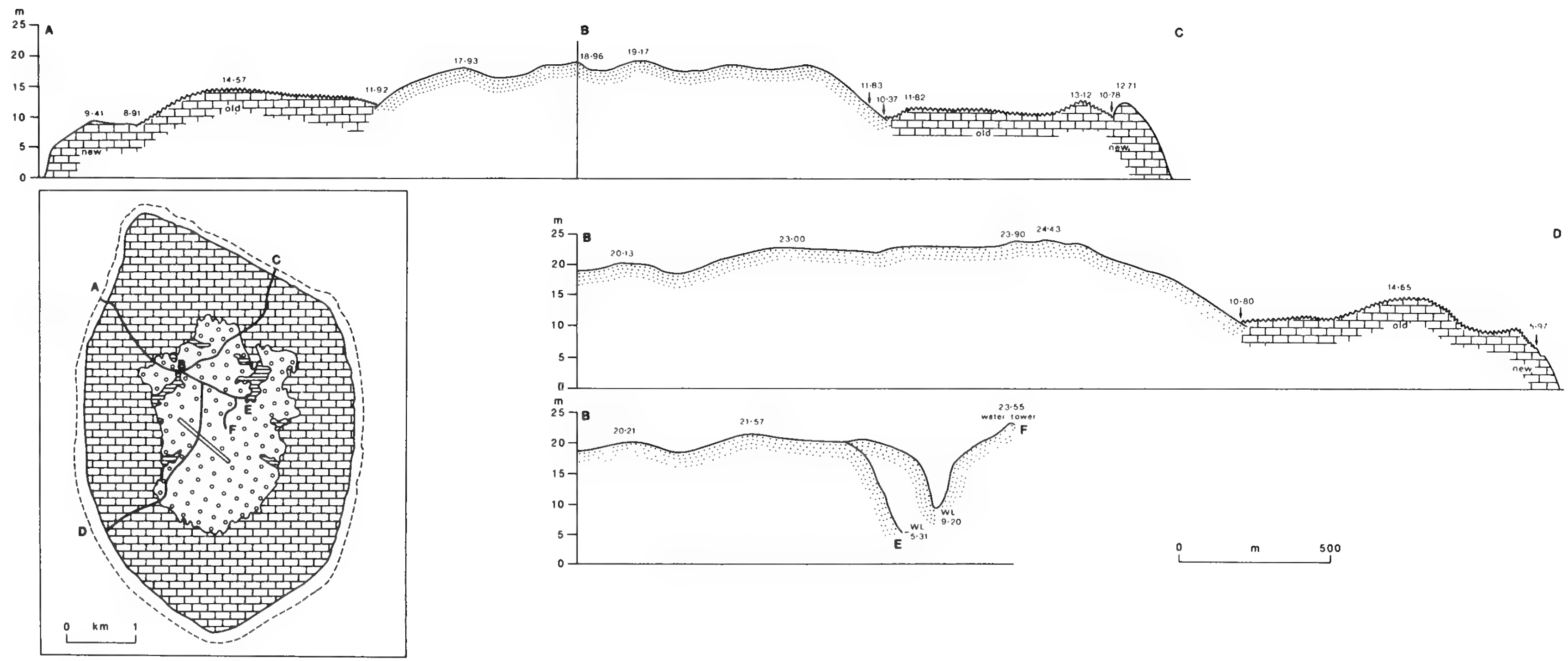


Figure 4. Mauke: topographic profiles AB, BC, BE, BF and BD

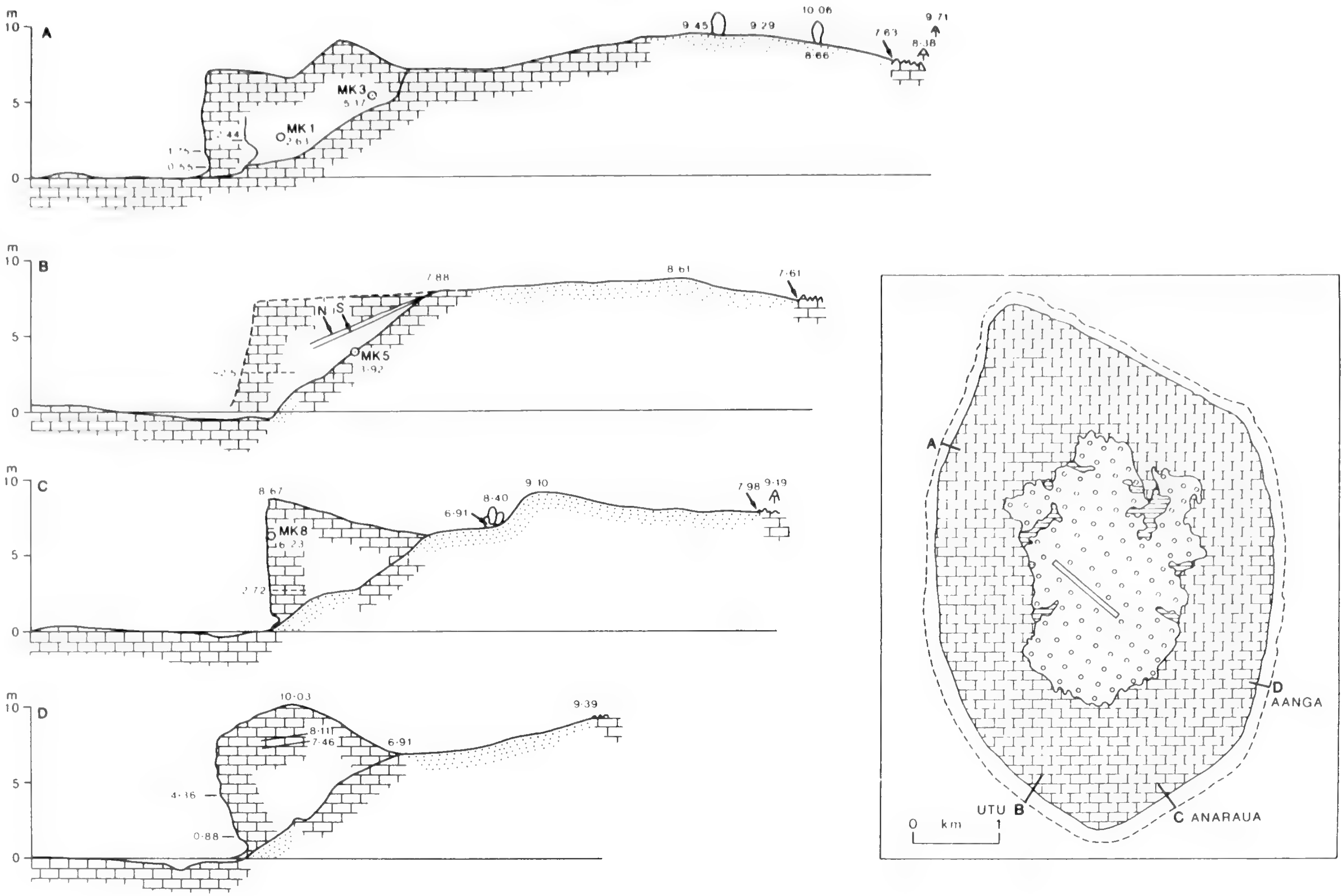


Figure 5. Mauke: topographic profiles A, B, C and D

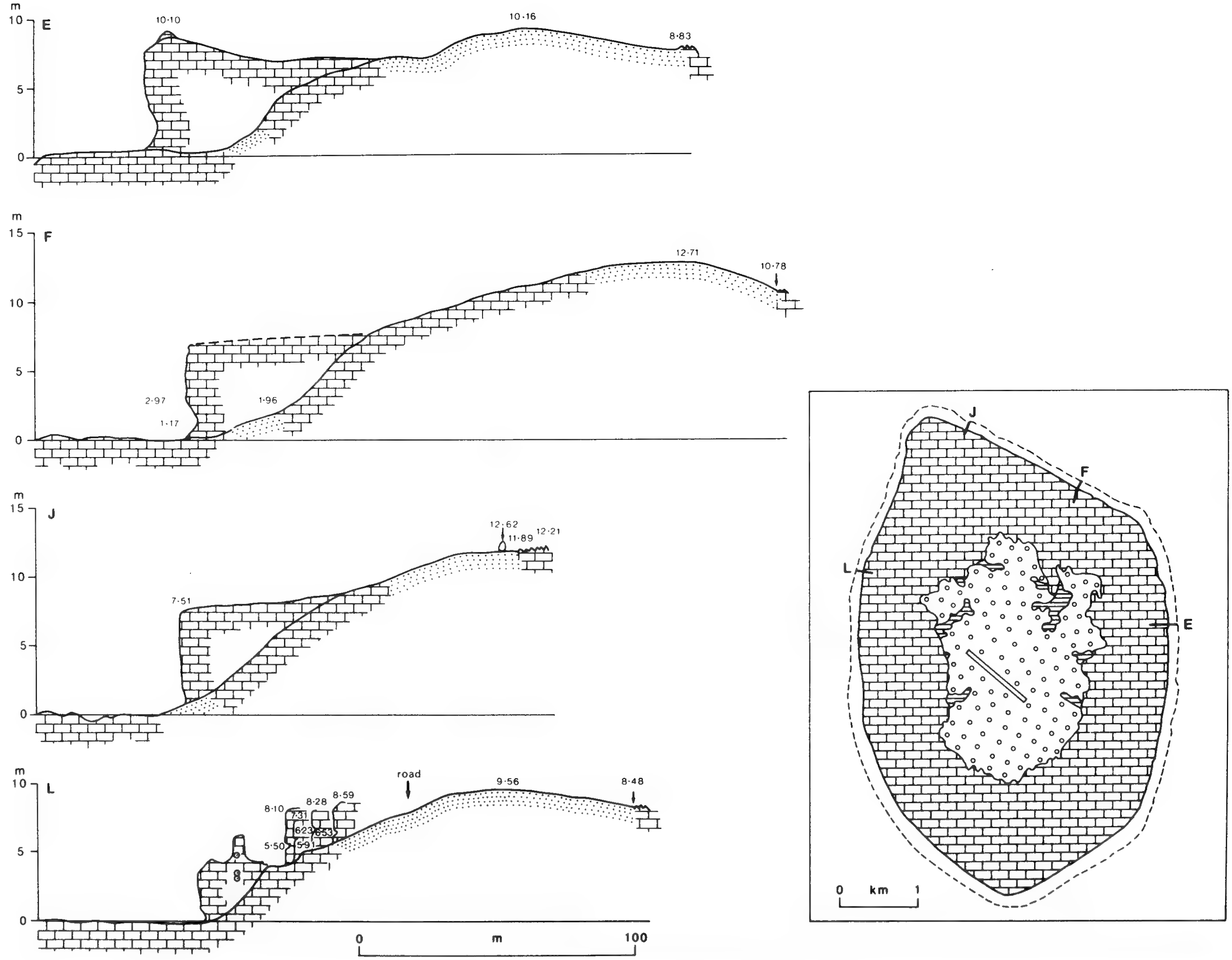


Figure 6. Mauke: topographic profiles E, F, J and L

Figure 7. Emerged groove-and-spur coastline at Taunganui, Mauke

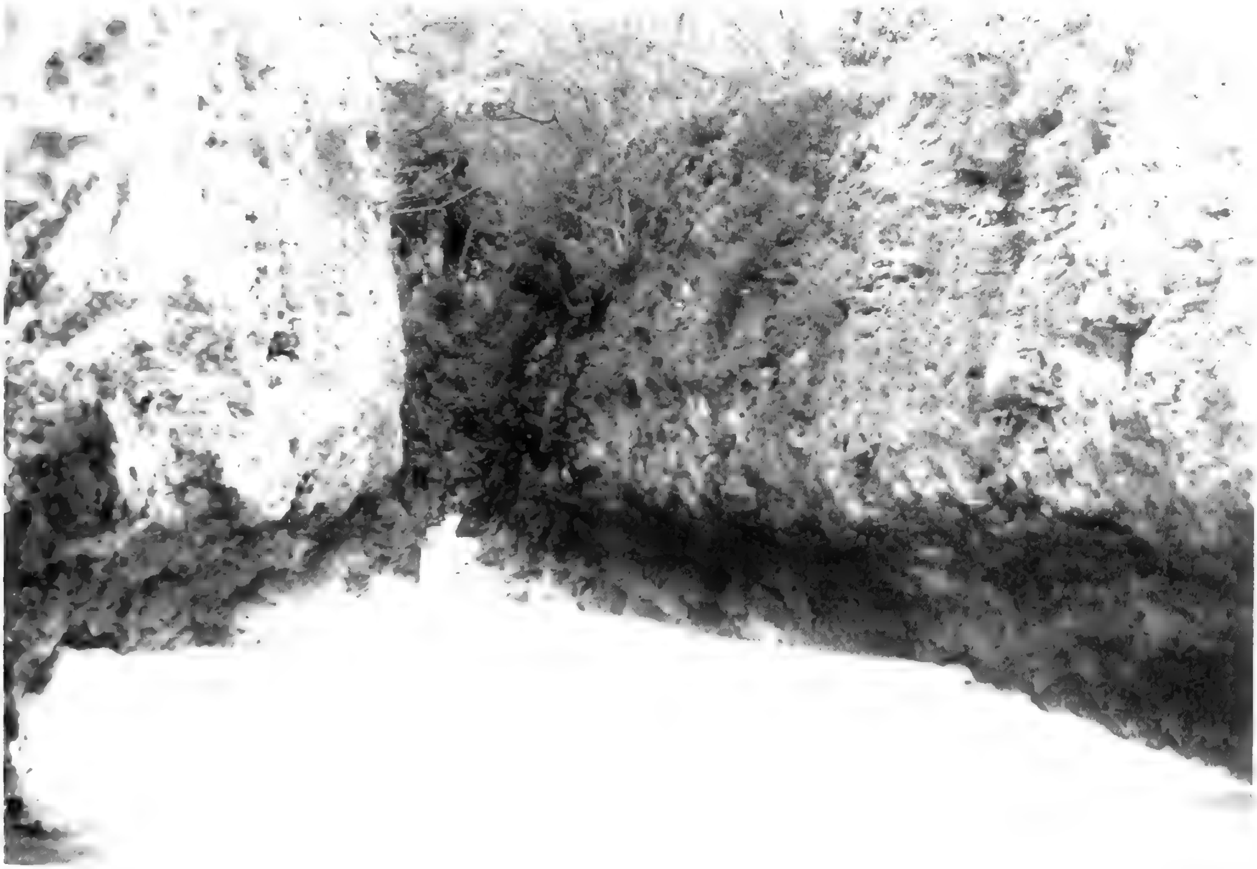


Figure 8. Groove in profile A at Taunganui, Mauke

Figure 9. Erosional embayment in coastal cliffs at Taunganui, Mauke

Figure 10. Perched boulder on profile A, Mauke

Figure 11. Detached coastal block, east coast of Mauke

Figure 12. Elevated reef flat near Aanga, Mauke

MITIARO

The island of Mitiaro (figures 13 and 14) is located at latitude 19°01'S., longitude 157°03'W., 225 km northeast of Rarotonga. It has maximum dimensions of 6.3 x 4.4 km. It stands on the summit of a conical volcano 4.25 km high, and approximately 25 km in diameter at its base (Summerhayes and Kibblewhite 1969). Grange and Fox (1955, 25) and Wilde (1981, 5) give its total surface area as 10.25 and 10.12 sq km, respectively, but planimetry of the New Zealand Department of Lands and Surveys 1:25,000 topographic map (1983) gives a total area of 29.56 sq km, comprising 22.47 sq km of elevated limestones, 1.27 sq km of volcanics, and 5.8 sq km of swamp and lake.

Volcanics

There are four discrete areas of low volcanic topography in the centre of the island. Three of these (the Atai and Auta foodland, the Taurangi foodland, and the Mangarei foodland) are completely encircled by marsh deposits in the centre of the island. The fourth, the Takuae foodland, is partly encircled by raised limestones, except on its northern side where it abuts the swamp. The maximum height of these volcanic residuals is quoted by Wood and Hay (1970, 35), Wilde (1981), and Turner and Jarrard (1982, 202) as 12 m; Grange and Fox (1955, 25) place it 'at or a little above the height of the makatea'.

Our topographic profiles (Figures 15 and 16) suggest that some of these elevations are exaggerated. Table 3 summarises available height information (which on the Lands and Surveys 1:25,000 map is photogrammetrically derived).

Table 3. Maximum heights of volcanics on Mitiaro

Area	Wood and Hay (1970)	1:25,000 map	this survey
Atai and Auta	3.0 m [10 ft]	4.0 m	3.9 m
Taurangi	-	5.0 m	5.7 m
Mangarei	9.1 m [30 ft]	3.0 m	6.9 m
Takuae	12.2 m [40 ft]	6.0 m	8.9 m

There are no outcrops of unweathered basalt on the volcanic residuals, which are covered with deeply weathered red and brown clays (Wilde 1981). Turner and Jarrard (1982, 193, 202) obtained a K-Ar age of 12.3±0.42 million years on a cobble of olivine basalt from the weathered material; because of alteration this must be considered a minimum age.

Interior depression

The extensive interior depression consists of a sedge marsh (Punavai) with *Cladium jamaicense* and a shallow open lake, Te Rotonui (figure 22). The water level in the lake stood at 0 m at the time of our survey, and in the sedge marsh at up to +0.4 m. Wood and Hay (1970, 35) refer to the marshes as 'a few feet above sea level', but this must be exaggerated. We have no information, however, on water-level variation.

Limestones: makatea

The greater part of the peripheral raised limestone of Mitiaro comprises deeply dissected makatea, presumably Cenozoic in age. There is some variability in existing estimates of the maximum elevation of this makatea. Grange and Fox (1955, 25) estimate it as less than 20 ft [6.1 m]. Wood and Hay (1970, 35) give the greatest elevation as 30 ft [9.1 m] but also give spot heights of up to 40 ft [12.2 m] on their accompanying map. The 1:25,000 Lands and Surveys topographic map gives spot heights of 15 m in the southeast, 11 m in the southwest, 12 m in the northeast, and 9-10 m elsewhere. McNutt and Menard (1978, 1208) in their theoretical analysis of island uplift use a figure of 27 m for the uplift of the limestones on Mitiaro. Jarrard and Turner (1979, 5693) and Turner and Jarrard (1982, 202) cite 15 m, and Lambeck (1981, 485) 12 m.

In our surveyed profiles across the makatea the greatest measured elevations are 10.9 m between Omutu and Atai (figure 16), 8.9 m between Omutu and Mangarei (figure 15), and 8.8 at Parava (figure 17). There is, however, a considerable area on the south side of the island in which we have no surveyed elevations and which is very difficult of access. Our data do, however, confirm the fact that the highest makatea is at the same level or higher than the maximum height of the volcanics. Grange and Fox (1955, 26) drew attention to the presence of 'large blocks of limestone on the margin of the Mangarei "island"' and suggested that the makatea formerly covered the whole of the centre of Mitiaro and was eroded during a period of lower sea level, thus unroofing and exposing the volcanics. Wood and Hay (1970, 35) likewise note the presence of 'coral blocks ... upon the highest parts of these [volcanic] "islands" and also around the margins of the swamplands surrounding them', and they reach a similar conclusion.

We have determined the elevation of the makatea-volcanics contact on the Mangarei and Takuae floodlands. On the north side of Mangarei it stands at 2.93 m and on the south side at 0.92 m above sea level. On Takuae there are elevations of 6.48 m (6.22 m for isolated scattered blocks) on profile F, section C-D, and of 5.10 and 4.79 m on profile F, section C-E. These heights are consistent with the solutional formation of the interior depression.

The surface morphology of the Mitiaro makatea is less pinnacled and rugged than on other islands, with more rounded terrain (Wood and Hay 1970, 35; Wilde 1981).

Limestones: Pleistocene

The coastal margins of the raised limestones are formed of much younger limestones, probably of late Pleistocene age. The peripheral cliffs are highest in the east (6.04 m in profile C, 6.67 m in profile D) and southwest (7.01 m in profile J), and lowest in the north (3.51 m in profile G) and west (2.73 m in profile H); we have not seen the cliffs along the south coast. Inland from the cliff top the surface increases in height,

usually to a maximum of 6-7.5 m (6.17 m in profile C, 7.40 m in profile D, 5.89 m in profile H, 7.73 m in profile J, 6.16 m in profile L), before passing beneath modern cover sands. The sequence from the cliff top to the cover sands consists of a complex microtopography of hummocks, gullies and broader depressions which contains abundant, well-preserved corals in the position of growth (e.g. Vaikoura). Uranium-series ages to be reported elsewhere indicate ages older than the last interglacial (ca 125,000 yr). Unfortunately the cover sands generally obscure the contact between the clearly Pleistocene coastal sequence and the makatea which it abuts and overlies. The relationship between the Pleistocene sequence and the underlying makatea is further obscured by the fact that the upper surface of the makatea lies close in many areas to the maximum height of the late Pleistocene deposits. This is well seen both on the transect from sea to lagoon at Parava (figure 17), where there are fields of late Pleistocene acroporid corals (figure 28), deeply weathered with apparent recrystallization of skeletal aragonite to calcite, but in the position of growth, at elevations of 6.77-7.81 m above sea level, especially on flat-lying areas and in depressions on the makatea surface, with older ridges and pinnacles of makatea reaching higher levels. Similarly, on the northwest coast (profile H), corals are abundant in grooves in the makatea surface but are absent from the highest areas between (corals in grooves stand at 3.65 m above sea level, compared with 4.09 m between).

Elevated subhorizontal transverse grooves are well developed above the cliff top in profile C (figures 26 and 27). Individual grooves begin at an elevation of 4.6 m at the cliff top and rise inland until they coalesce into a continuous rocky ramp parallel to the cliff edge at a height of 5-5.6 m. The grooves are margined by an undercut notch with a visor at 5.0 m above sea level. Between these flat-floored grooves there are irregular ridges rising to 6-6.2 m.

Similarly, in profile L, there is a sequence of groove-and-spur features on the cliff top, with coral growth within the grooves. Some of the grooves are roofed-over and closed at their seaward exit; others are open with undercut, smoothed walls (figure 24). There is a pronounced discontinuity in the cliff face at this point between a lower and an upper limestone unit. This discontinuity rises from 2.62 m above sea level in the north to 4.45 m in the south, over a distance of 50 m. The discontinuity forms the flat floors of the grooves. The floor elevations also rise inland: in one sample groove, with the floor at 3.81 m above sea level at the cliff line, the floor rises to 5.68 m inland over a distance of 20 m. The upper unit forms the spurs between the grooves. At the cliff line this unit is 1.24-2.10 m thick. The upper surface of this unit also rises inland: at the same location it stands at 4.69 m at the cliff line and rises inland to 6.27 m over 20 m. Grooves at other localities have floors at 4.8-5.0 m above sea level in profile B and at 3.65 m in profile E.

Comparable discontinuities between upper and lower limestone units are found at varying heights around the coast: at 5.6-6.0 m in profile B, 4.1-4.75 m in C, and 5.0-5.1 m in D.

Coastal morphology

There is a continuous reef flat around the island, averaging 100 m in width and reaching a maximum of 120 m. It is edged by a prominent algal ridge, with deep surge channels. The datum used in this study is the lowest elevation of an identifiable algal ridge; the maximum elevation of the highest algal ridge we have measured rises 0.83 m above this datum (profile K; figure 21). Contemporary reef flat surfaces, all of eroded limestone with little sediment cover, lie at or close to datum, with two exceptions. The first is that all along the west coast there are extensive residuals on the reef flat of a higher surface. In profile K these stand up to 1.23 m above datum, as steep-sided platforms with pitted and

eroded upper surfaces (figures 31 and 32). These residuals may represent a fossil algal ridge, similar to those described from Mangaia, southern Cooks (Yonekura et al. 1986, 1988) and Suwarrow, northern Cooks (Scoffin et al. 1985), indicating the former position of the reef margin prior to the Holocene sea level highstand of ca 1.0 m between ca 6000-2000 a B.P. in this part of the Pacific (Pirazzoli and Montaggioni 1988). Second, in most profiles the reef flat is more deeply scoured at the foot of the cliffs, often forming pools which retain water even at low tide and which is some cases contain massive living microatolls, especially of *Porites*. In profile K these pools are scoured down to -1.34 m below datum, and the tops of the microatolls (figure 33) stand at +0.10 and +0.13 m.

The cliffs are generally conspicuously notched at or slightly above the present reef flat level. Most notch floors stand close to this level, with the deepest part of the notch at elevations of 0.5-1.0 m above it (0.56 m in profile J, 0.63 m in G, 0.83 m in K, and 0.97 m in H). Visor elevations range more widely, doubtless reflecting local exposure (e.g. 1.97 m in profile H, 2.23 m in G, 3.16 m in J, and 3.23 m in K). Most notches are 2-3 m deep.

In profile D there is a comparable but higher notch (figure 25), with its floor at 1.77 m, its deepest part at 2.27 m, and its visor at 4.07 m; this notch has a horizontal extent of 5.0 m.

There are occasional pocket beaches of carbonate sands and gravels in indentations in the cliffs. The foot of these beaches lies at survey datum (e.g. +0.05 m in profile K).

Holocene coastal features

The cover sands above the cliffs, already noted, form a perched beach back from the cliff edge round most of the island (figures 29 and 30). They form some of the highest ground of the island. Elevations on the cover sands reach 9.76 m in profile D, 10.10 m in E, 10.2 m in G, and 10.9 m in B. The sands have not been trenched but are probably 1-2 m thick. They are usually 100 m wide but in places exceed 200 m and exceptionally reach 500 m.

Large perched boulders of reef rock, undoubtedly of storm origin, are common round the entire coast of the island. The biggest recorded, 2.2 m high, stands 100 m back from the cliff top in profile H at an elevation of 4.85 m. Another in profile B is 1.67 m high and lies 47 m from the cliff top at an elevation of 6.75 m. Two in profile C are respectively 1.3 and 1.7 m high, at 9 and 35.5 m from the cliff top, at elevations of 6.17 and 5.11 m above sea level. In some cases they show inverted coral colonies. They appear to be relatively recent: they are not deeply eroded on their upper surfaces, and they do not stand on protected pedestals of underlying limestone. W. M. Gill noted that the hurricane of 1865 brought wave action up to 30 ft [9 m] above present sea level (Grange and Fox 1955, 26), and such events, though not necessarily that particular one, have doubtless been responsible both for the deposition of the perched beach sands and for these storm blocks.

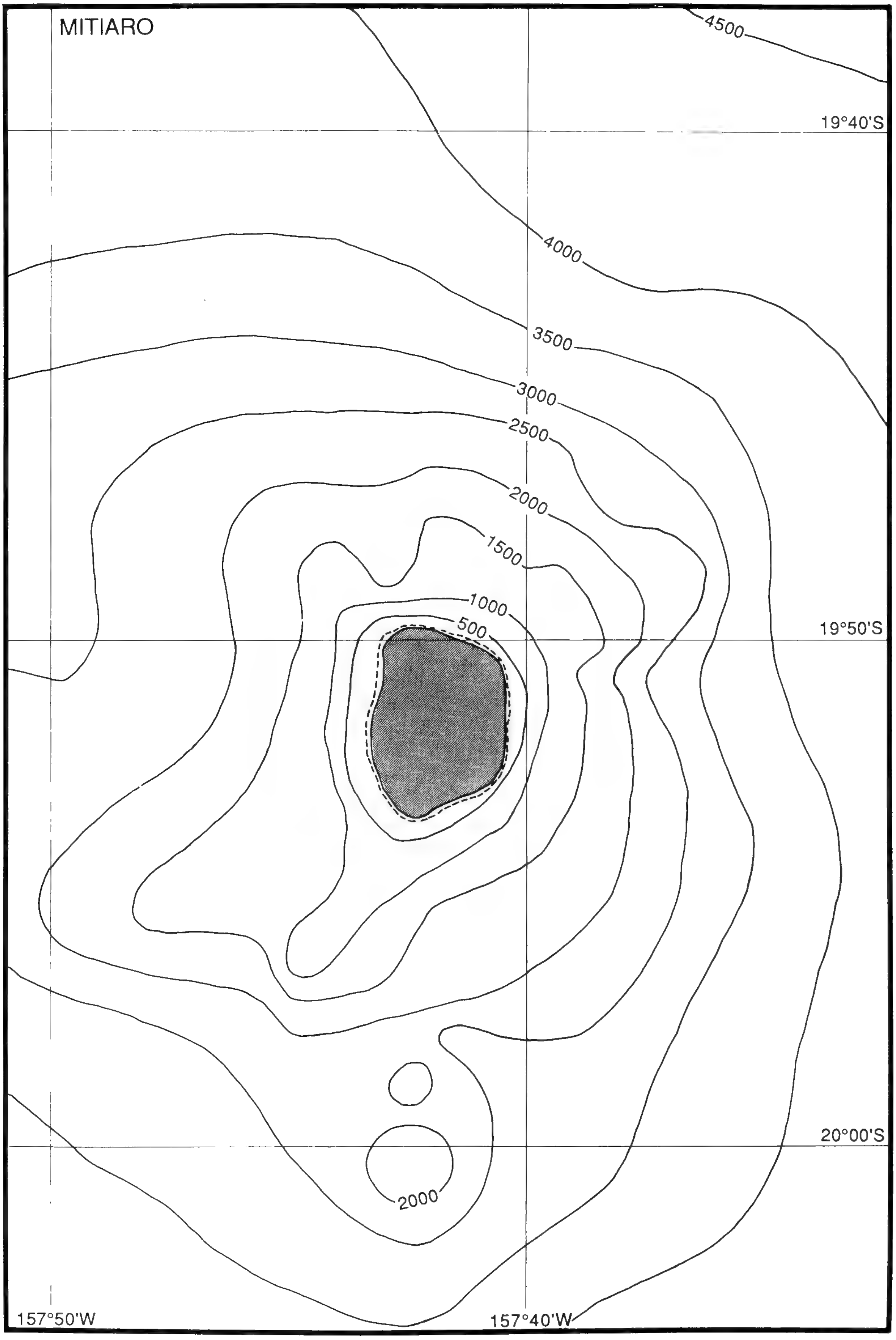


Figure 13. Bathymetry of Mitiaro (after Summerhayes and Kibblewhite 1968)

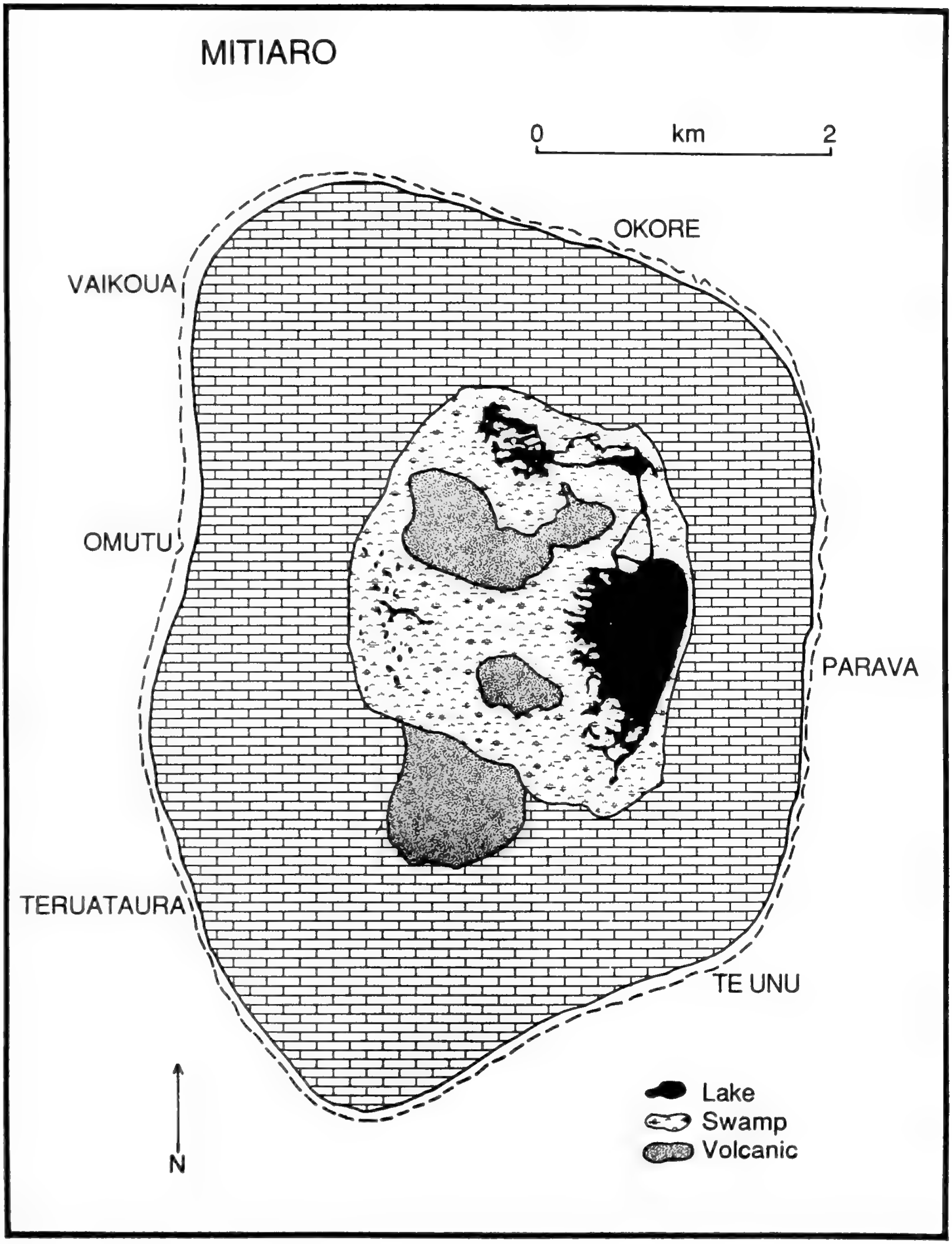


Figure 14. Geology of Mitiaro

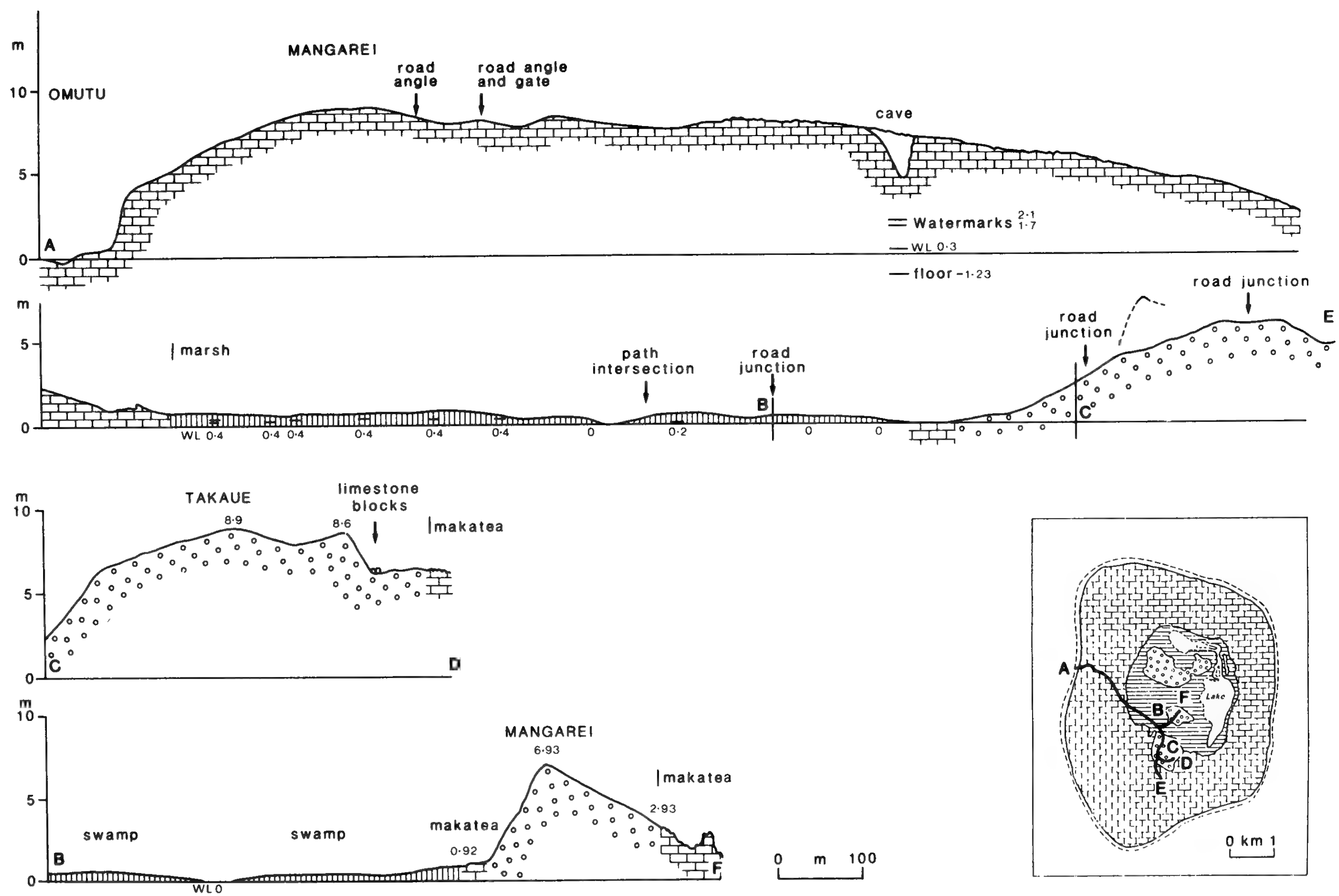


Figure 15. Mitiaro: topographic profiles AB, BD, BE and BF from the coast to Takuae and Mangarei

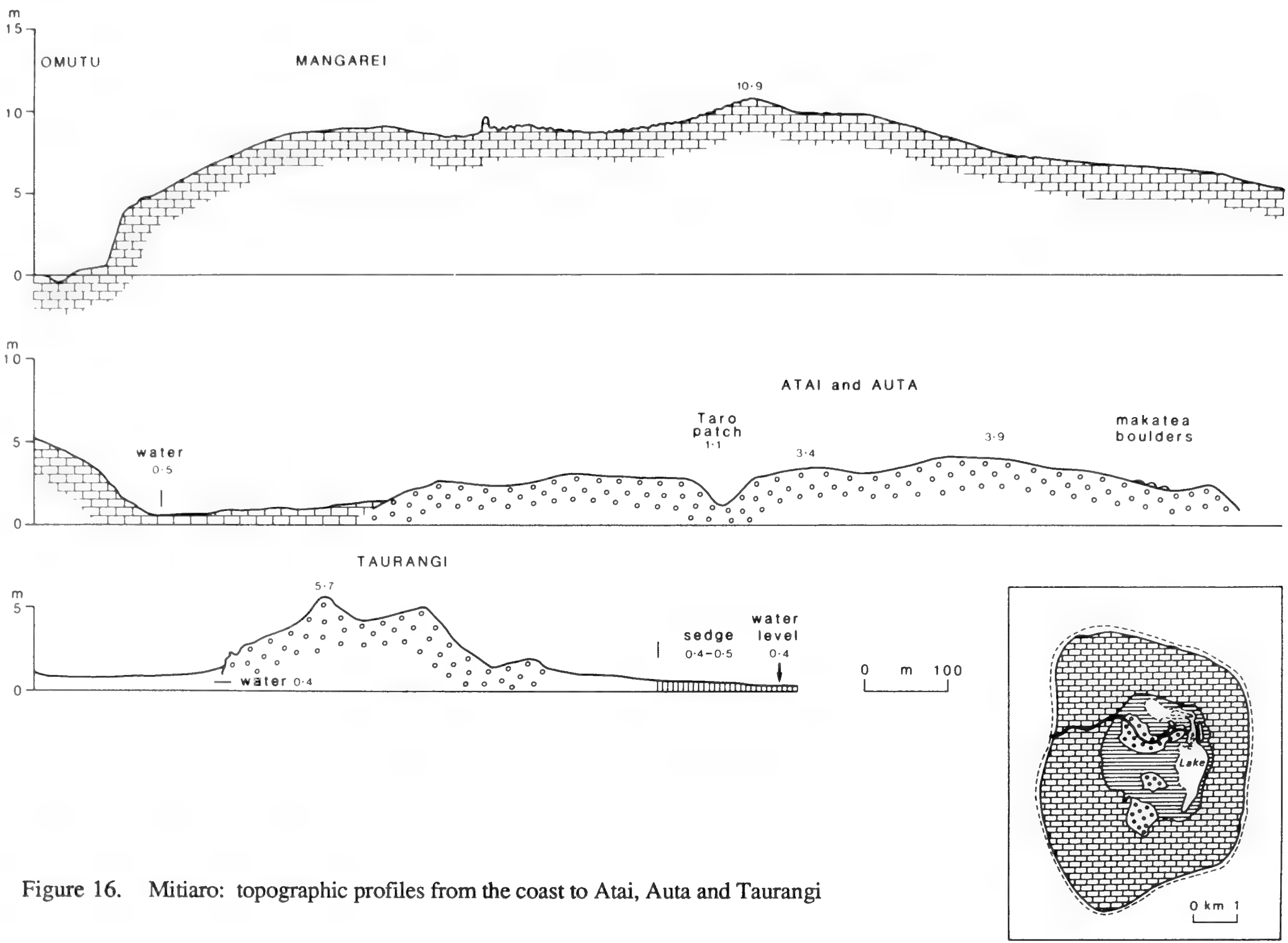
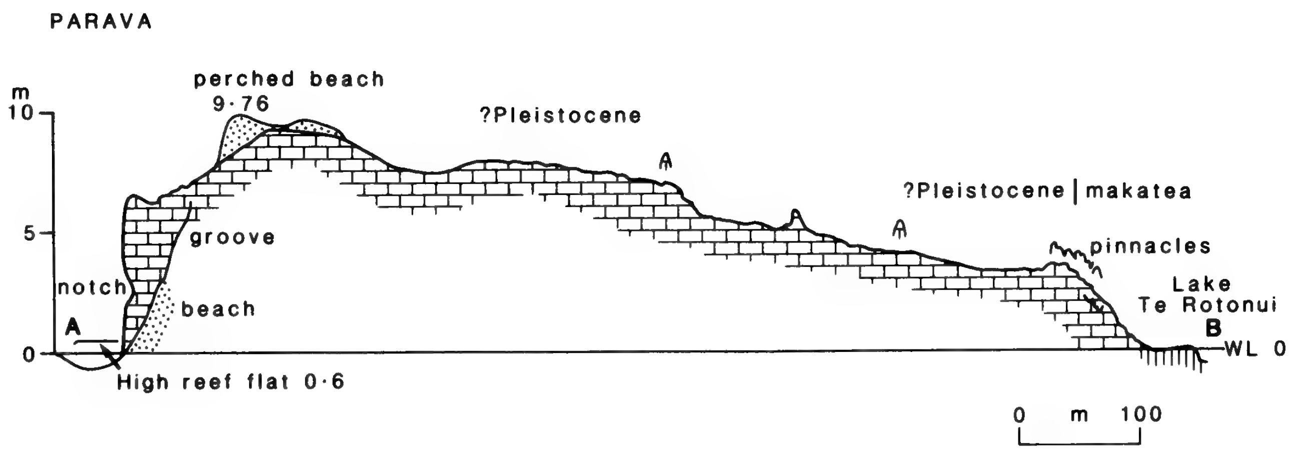


Figure 16. Mitiaro: topographic profiles from the coast to Atai, Auta and Taurangi



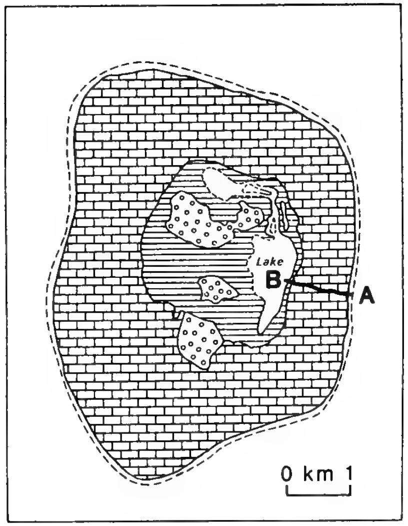


Figure 17. Mitiaro: topographic profile across the makatea rim at Parava

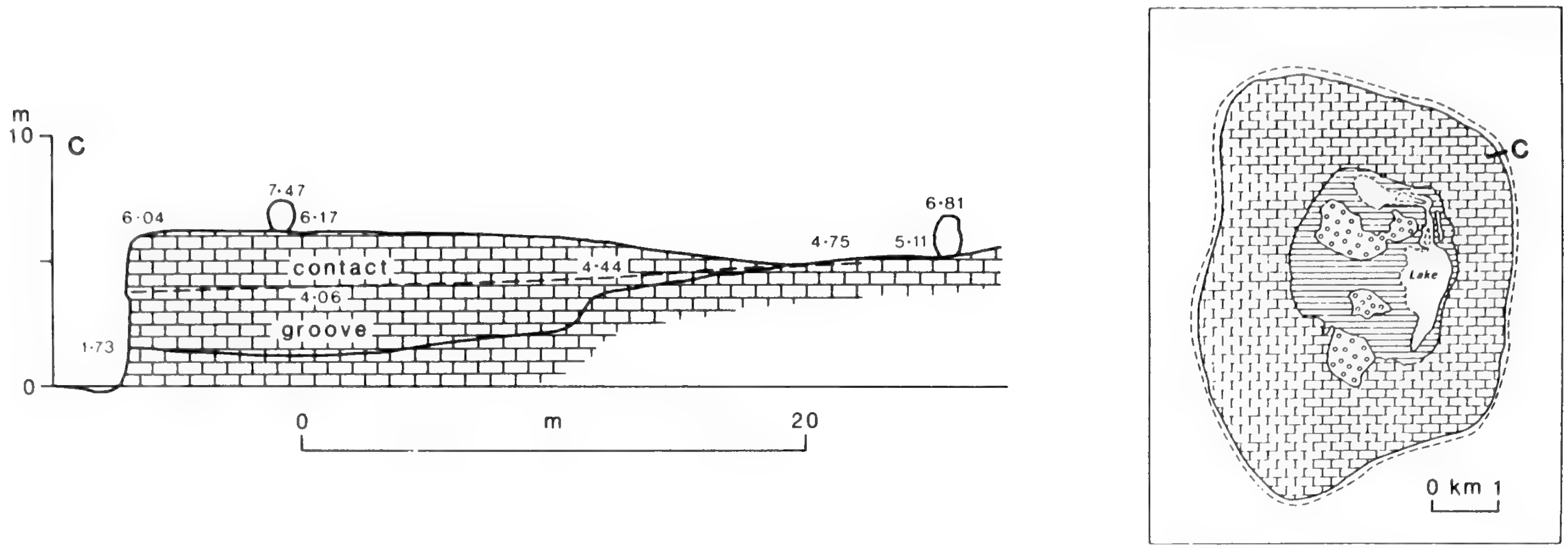


Figure 18. Mitiaro: topographic profile C (groove-and-spur)

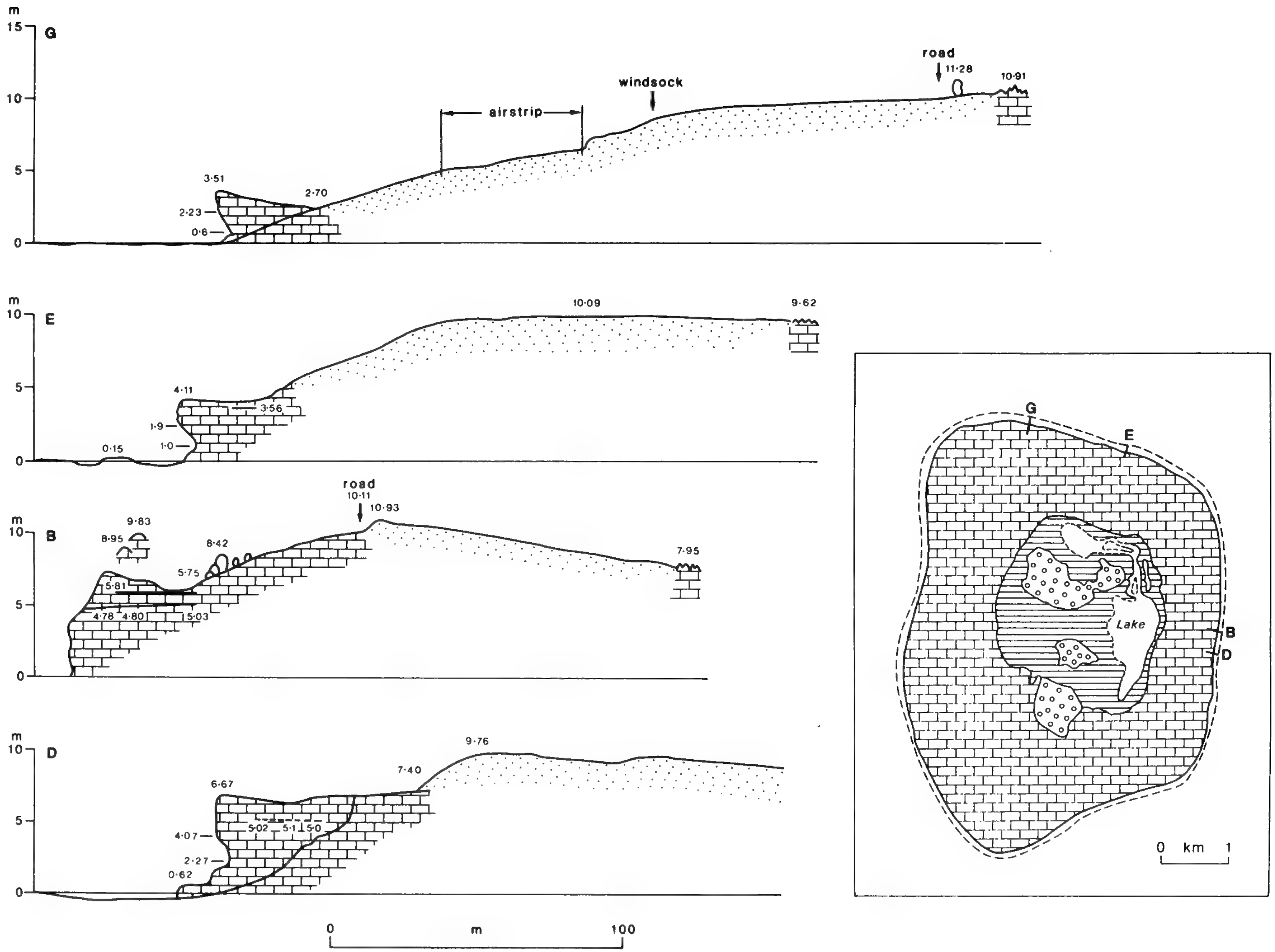


Figure 19. Mitiaro: topographic profile G, E, B and D on the north and east coasts

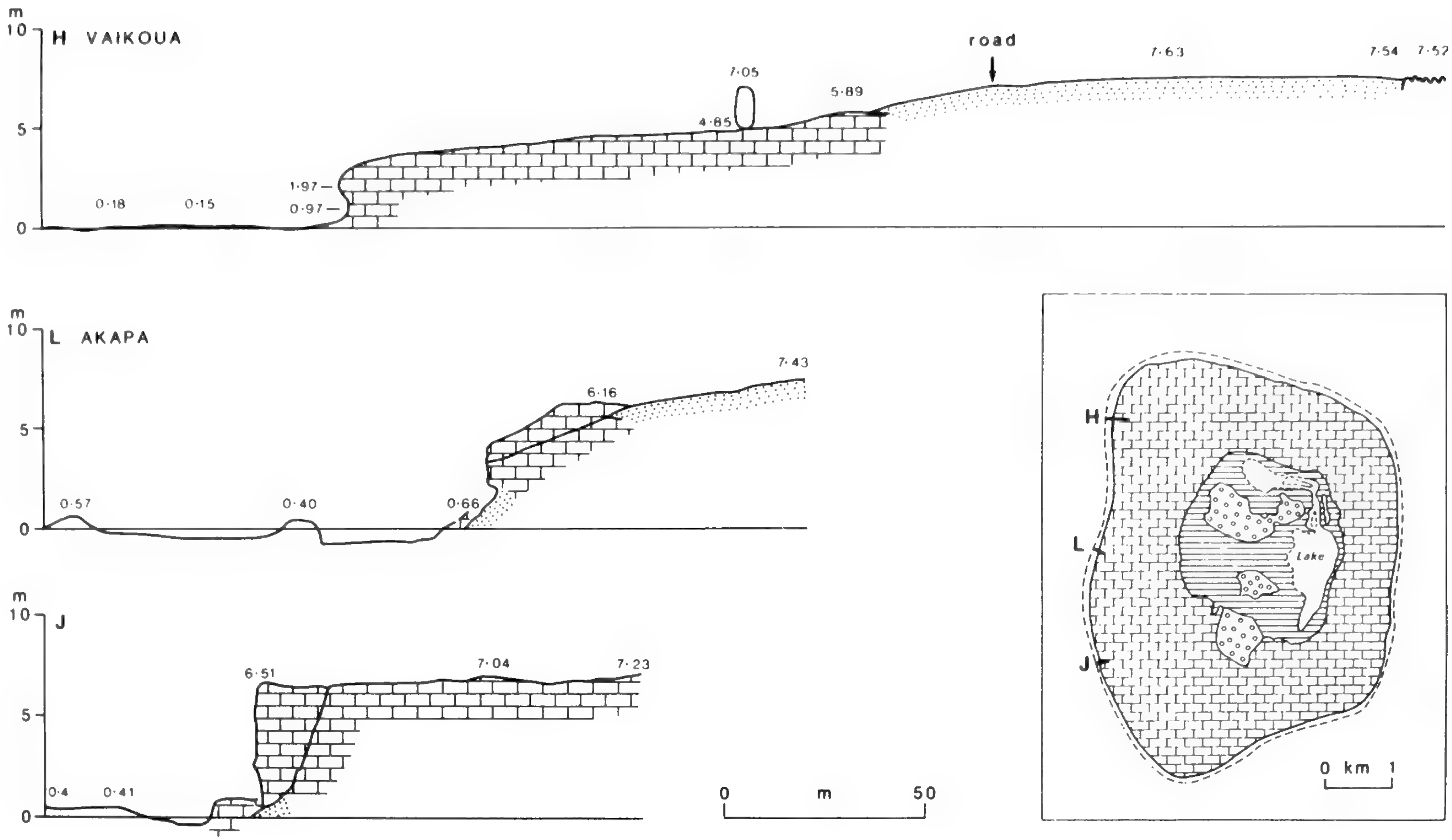


Figure 20. Mitiaro: topographic profiles H, L and J on the west coast

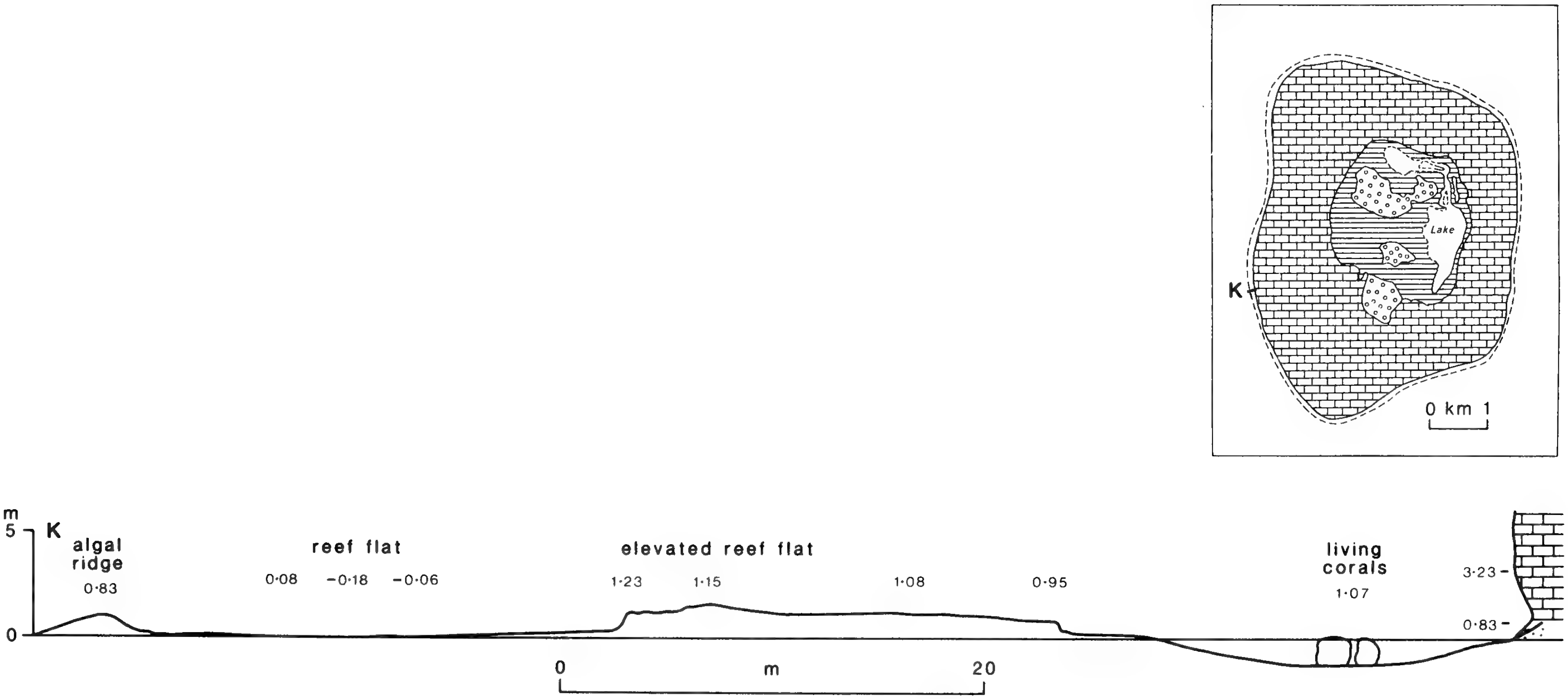


Figure 21. Mitiaro: topographic profile K on the reef flat at Tukume

Figure 22. Te Rotonui and the central volcanics at Mitiaro, from the west end of profile AB

Figure 23. Coastal cliffs near Omapere, Mitiaro

Figure 24. Emerged groove in coastal cliffs at Teruataura, northeast coast of Mitiaro

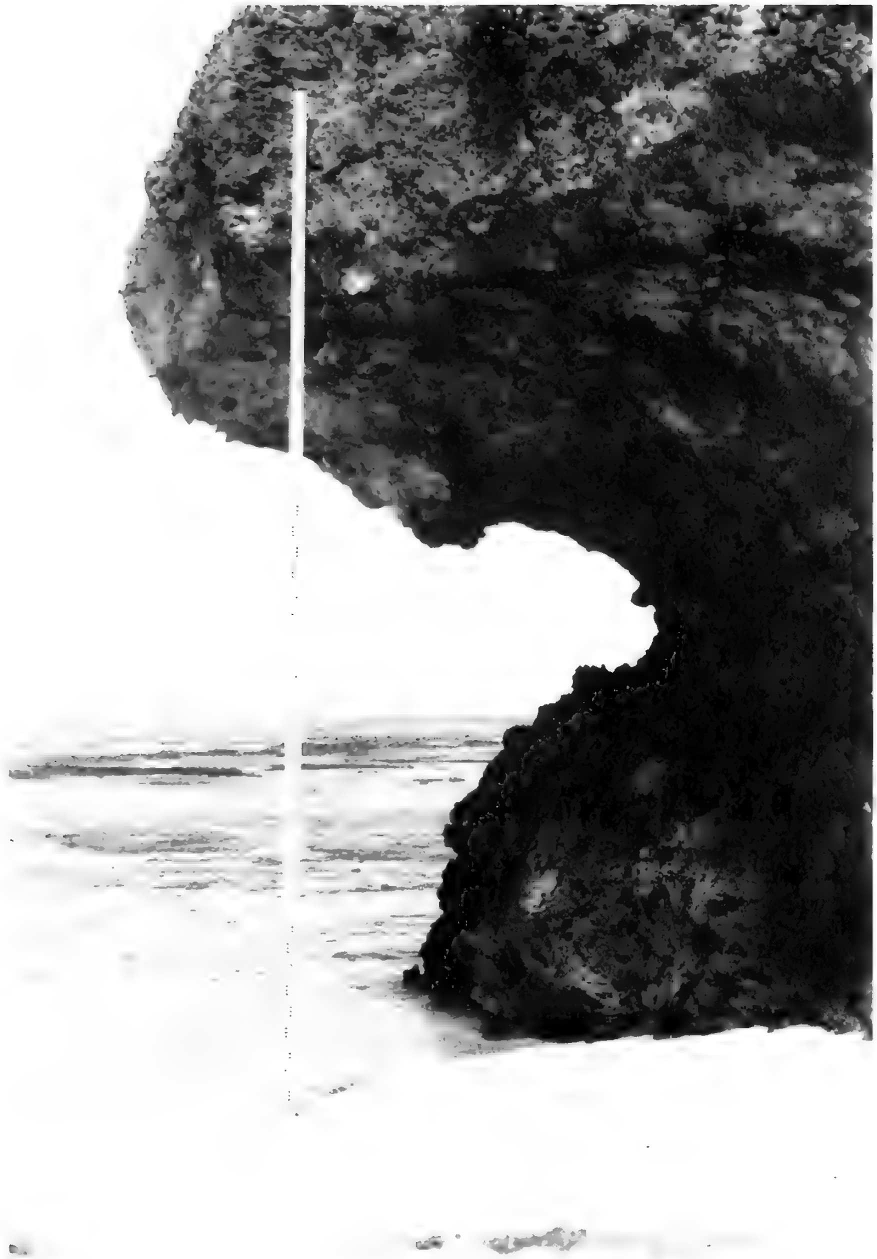


Figure 25. Elevated notch at Parava, Mitiaro, at profile D. The deepest part of the notch stands at 2.27 m and the visor at 4.07 m.

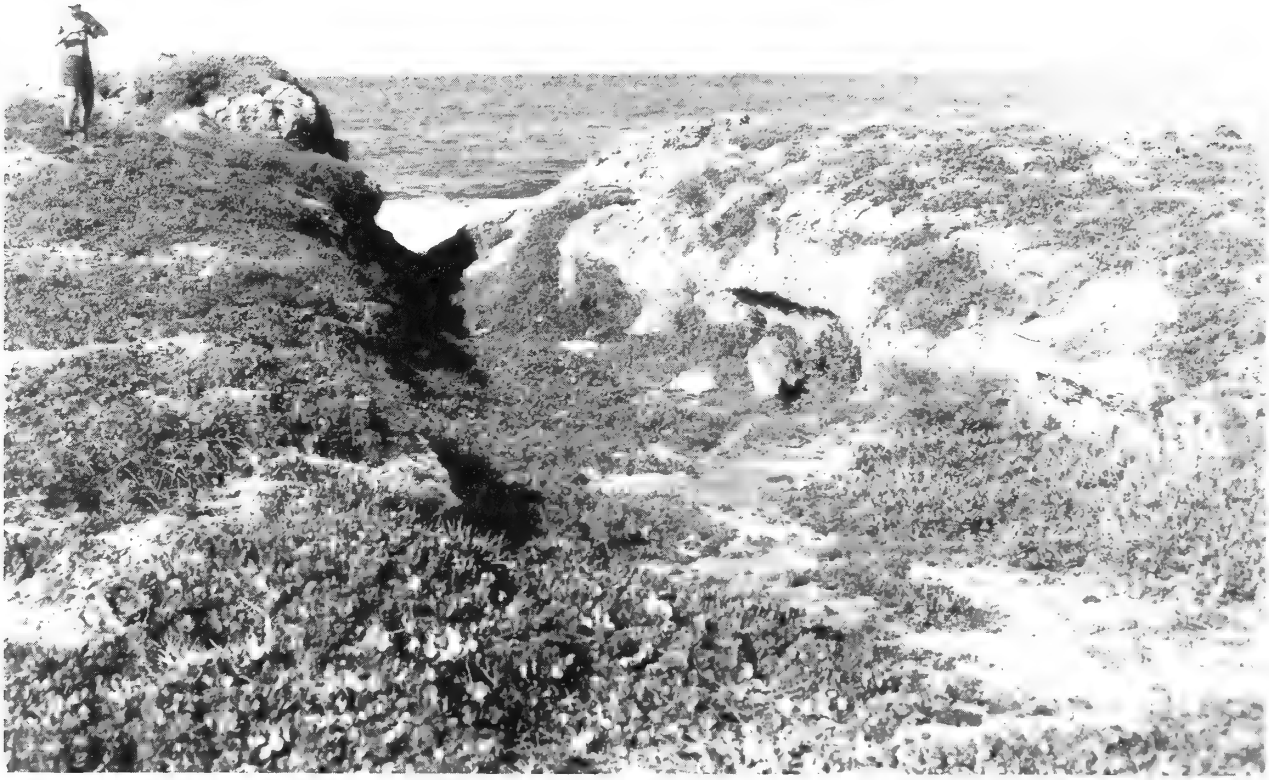


Figure 26. Cliff-top grooves with basally-notched walls, profile B, Mitiaro. The floor of the grooves stands at 4.78-5.03 m.

Figure 27. Cliff-top abrasion platform at 5.75 m with cover of storm blocks on its landward side, profile B, Parava, Mitiaro

Figure 28. Emerged *Acropora* on the makatea surface at Parava, Mitiaro

Figure 29. Storm block on profile C, Mitiaro. The base of the block is at 6.17 m.

Figure 30. Storm block on profile H, at Vaikoua, Mitiaro. The base of the block is at 4.85 m.

Figure 31. Raised reef flat at Oponui, Mitiaro

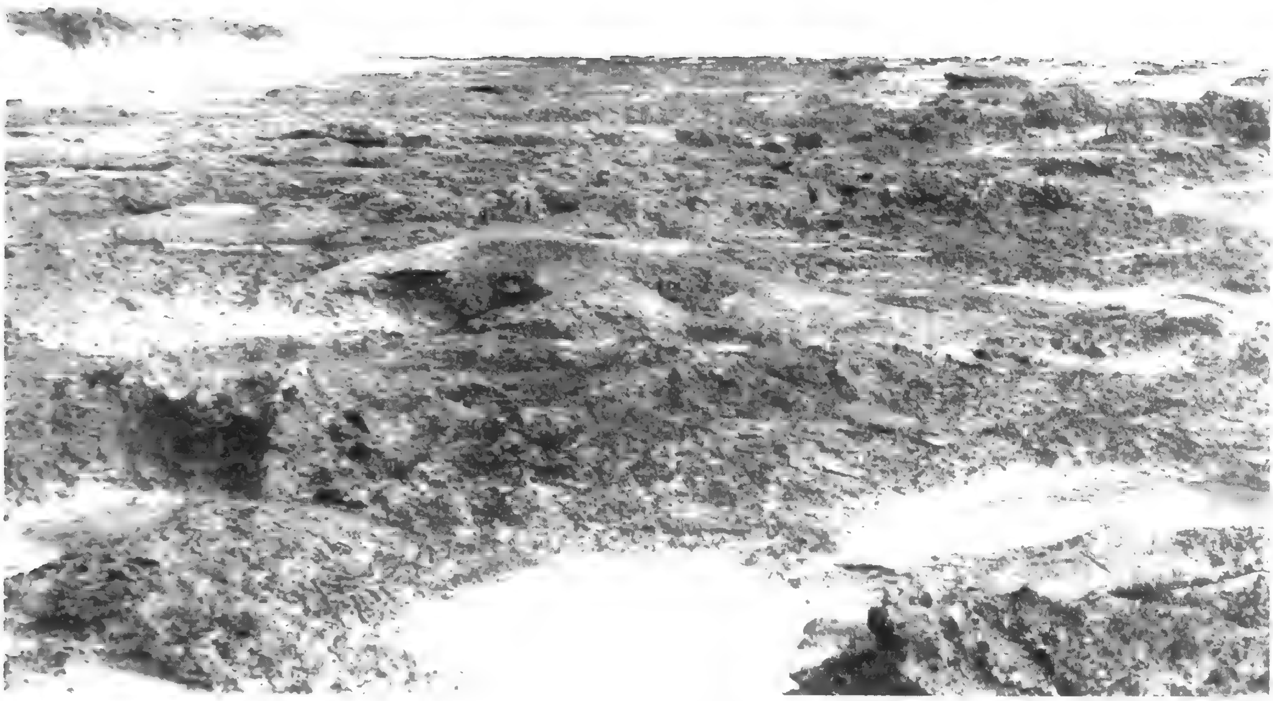


Figure 32. Raised reef flat at Vaikoua, Mitiaro

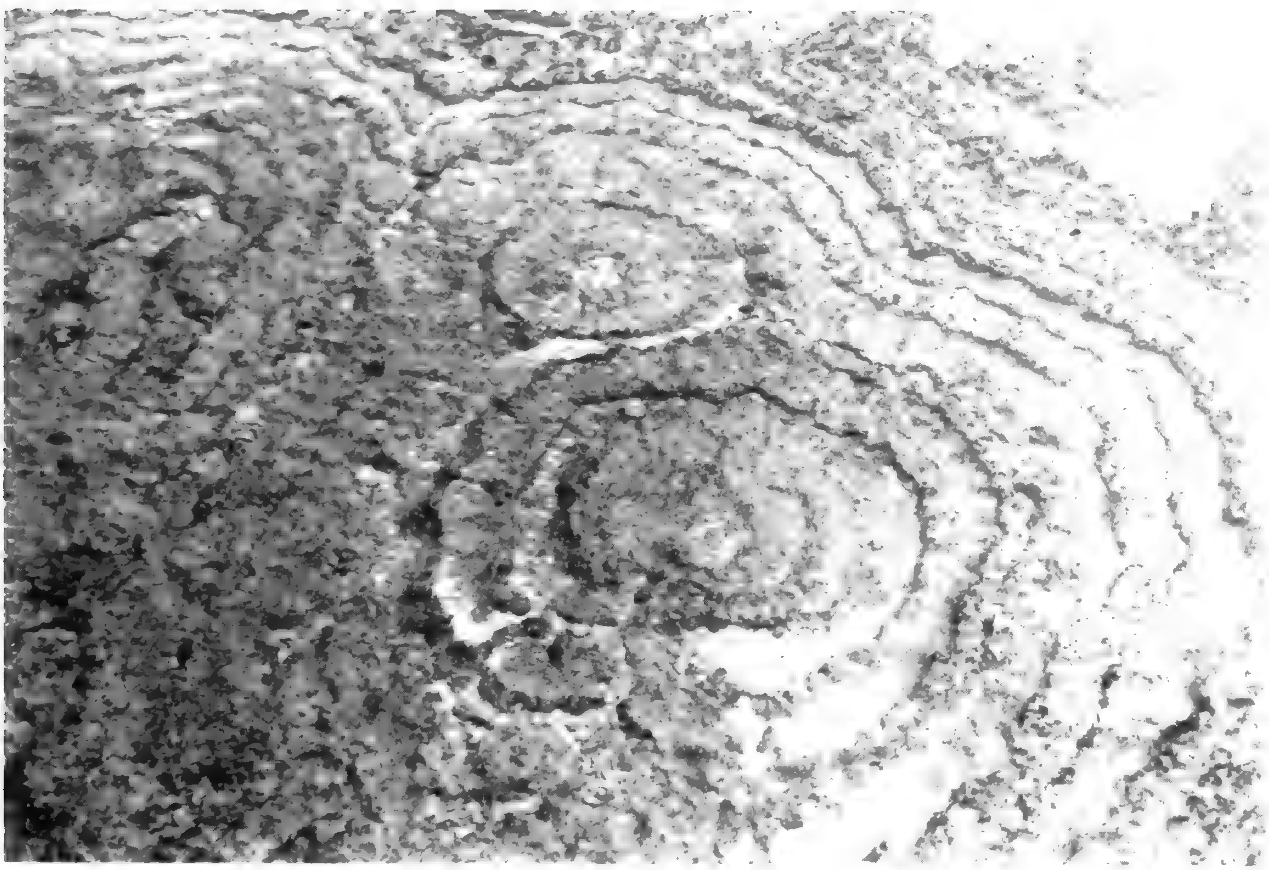


Figure 33. Microatolls in cliff-foot pool, seen from the cliff top, at Vaikoua (profile K), Mitiaro

Figure 34. Reef edge surge channel at Teruataura, west coast of Mitiaro

ATIU

Atiu, the largest and highest of the islands considered in this paper, is located in latitude 20°S., longitude 158°10'W., 187 km northeast of Rarotonga. It has been mapped photogrammetrically at 1:7920 by the Department of Survey, University of Otago (Hunt 1969). From this map the greatest dimensions of the island are 7.25 km N-S and 6.3 km E-W, compared with the 6.4 km [4 miles] and 6 km [3.75 miles] quoted by Grange and Fox (1955, 19). Its total area according to Grange and Fox (1955, 19) is 6654 acres [26.9 sq km] and from the topographic map 29.0 sq km. Like the other islands Mitiaro and Mauke, Atiu consists of an eroded central volcanic area surrounded by an elevated limestone rim. Unlike the other islands, however, Atiu was the subject of an extensive early account of its geology by Marshall (1930).

Volcanics

Atiu (figures 35 and 36) is the summit of a subconical asymmetric volcano some 25 km in diameter at the 3 km isobath (Summerhayes and Kibblewhite 1968). It is contiguous with Takutea to the northwest at the 3 km isobath, and with Mitiaro to the northeast at the 3.5 km level. The slopes of the Atiu cone are steepest to northeast and southeast.

The central volcanic area of the island comprises a flat-topped plateau, dissected by steep-sided, flat-floored radial valleys, well outlined by the 50 m contour (figure 39). Estimates of the height of the plateau vary. According to Schofield (1967, 119) it ranges from 65 to 82 m, the latter figure presumably deriving from Grange and Fox (1955). Wood and Hay (1970, 33) give a maximum figure of 235 ft [71 m], which is accepted by Turner and Jarrard (1982). Campbell (1982) quotes 72 m. The University of Otago topographic map gives a spot height of 70.97 m. We were unable during our time on Atiu to carry traverses from the coast through to the volcanics.

The basalts were first described by Marshall (1930, 7) and subsequently by Wood and Hay (1970, 33) and C. P. Wood (1978). Jarrard and Clague (1977) cite ages of 3.5-5 million years for these rocks, but these determinations have been superceded by those of Turner and Jarrard (1982). They report two group of dates: an older group of three, from 9.1±1.5 to 10.0±0.4 million years, and a younger group of four, from 8.0±0.2 to 8.4±0.3 million years. They infer two periods of volcanism at approximately 10 and 8-8.5 million years. Deep weathering has led to the formation of a red clay with limonitic nodules and black manganiferous veins (Wood and Hay 1970).

Since the time of Marshall (1930) many workers have drawn attention to the presence of terraces on the volcanic slopes, in addition to the bevelled summit. Marshall himself (1930, 70) identified a terrace at 70 ft [21 m] and a less pronounced terrace at 40 ft [12.2 m], which he considered to be of marine origin. Schofield (1967, 119) found 'terrace remnants' at 21, 12 and 4.6 m [70, 40 and 15 ft], which he also interpreted as 'marine platform levels'. Campbell et al. (1978, 231-232) describe a highest terrace, 700 m wide, rising to a height of 45 m with a 5° slope, bounded at its outer edge by a scarp 8-10 m high, followed by a second terrace up to 200 m wide, descending to 20 m above sea level, and finally a third terrace at 7-15 m. Later Campbell (1982) refers to the 'most prominent' terrace at 20-30 m, with 'smaller intermediate and lower terraces', each with distinctive soil assemblages. These features, which are not well supported by locational or altitudinal data, have been used to erect erosional histories for the island based largely on inferred sea-level change. Because of time constraints we could not investigate these

features on the volcanics, but it is crucial for the interpretation of the history of Atiu that their status be resolved.

The volcanics are for the most part covered with deeply weathered red and brown clays, described in detail by Campbell et al. (1978) and Campbell (1982).

Marginal swamps

Between the volcanics and the makatea is a discontinuous lowland, termed a 'moat' by Marshall (1930), where streams flowing from the dissected volcanics are ponded back by the peripheral limestones to form swampy areas. The most extensive of these marshes extends for 3.5 km along the northeast flank of the volcanics. Some have been converted to taro cultivation; others still have massive buttressed trees of *Inocarpus edulis*, the low herb *Ludwigia octovalvis*, or sedges. Marshall (1930) believed the swamps stood at 20-30 ft [6-9 m] above sea level, and these figures have been quoted by Wood and Hay (1970, 33). Campbell (1982) gives an elevation of 6 m, and Campbell et al. (1978, 231-232) 2-4 km. The Otago topographic map, however, gives heights of 6-10 ft [1.8-3 m].

There is one extensive freshwater lake, Tiriroto, in the southwest part of the island (figure 40). The Otago map gives the height of the water surface as 3 ft [0.9 m]. The inner wall of the makatea which bounds it on its west side is deeply notched, with a characteristically horizontal notch roof 1.0-1.5 m above the swamp surface. This notch is generally 1-2 m in horizontal extent, but locally reaches 5 m, and exceptionally 8 m (figures 41 and 52). Marshall (1930) and local informants say that seawater incursions occur through and under the makatea.

Limestones: makatea

Limestones of presumably Cenozoic age (Marshall [1930] dated them as early Pliocene and later) entirely surround the central volcanics. Marshall (1930) described them as 1200 yards [1100 m] wide, terminating seawards in cliffs 10-20 ft [3-6 m] high, rising to a height of 70 ft [21 m] within 300 yards [275 m] of the coast, and then declining to the level of the swamps in a distance of 600-800 yards [550-730 m]. Grange and Fox (1955) likewise describe seaward cliffs 30 ft [9 m] high, a makatea surface rising to a maximum height of 70 ft [21 m], and the limestones having a total width of 0.5-1 mile [0.8-1.6 km]. Campbell et al. (1979, 247) record the presence of 'fresh basalt fragments within the coral limestone at the present inner limestone margin', possibly indicative of reef growth while volcanism still continued. Wood and Hay (1970) quote an average width of 1100 m, seaward cliffs 6 m high, and maximum heights of 70 ft [21 m] in the south and 100 ft [39 m] in the north. Campbell (1982) and Campbell et al. (1978) also refer to cliffs 6 m high, but give a maximum elevation for the makatea of 30 m, in the centre, before the surface declines inland to elevations of 6-15 m.

The Otago topographic map clearly shows the broadly convex transverse profile of the makatea (figure 36). It also shows that the makatea is highest on the northwest and east where its central part exceeds 60 ft [18 m]. Two spot heights of 75 ft [23 m] are marked on the east side. Conversely, on the southwest and south sides, maximum elevations rarely exceed 50 ft [15 m]. There is a similar apparent tilt to the upper surface of the makatea on Mangaia, where the west side is some 20-25 m higher than the east (Stoddart et al. 1985, 123).

In places the inner margin of the makatea grades smoothly into the volcanic slopes (Grange and Fox 1955, 19), but elsewhere, especially adjacent to swamps, it is formed by a vertical cliff 10 or more meters high (Campbell et al. 1978, Campbell 1982), with dripstones and flowstones. At Kurekure these cliffs are 20-25 m high (not 20 ft [6 m] as reported by Marshall [1930, 68]). They are conspicuously notched at their base, with a 1 m high notch extending to a horizontal depth of 10 m in places. There are apparently no outliers of the makatea on the volcanics (Marshall 1930, 69; Campbell et al. 1979, 247), though Jarrard and Turner (1979, 5691) refer to 'a few outcrops ... on the central volcanic hills', apparently at an elevation of 55 m (Jarrard and Turner 1979, 5693). This is 32 m above the present maximum elevation of the makatea proper; until these outcrops are confirmed or properly described, this report must be discounted.

Campbell (1982, 8) states that the makatea surface 'rises inland by a series of gentle steps ... [which are] possibly marine benches'. We did not have the opportunity to investigate these.

On the basis of foraminifera, Marshall (1930) suggested that the inner (older) section of the makatea was equivalent in age to the outer section of the makatea on Mangaia, i.e. early Pliocene. He also (1930, 56-57) found mineralogical differences in the limestones, with the older (inner) limestone being dolomitized. In 1985 Woodroffe found dolomitic crusts up to 3 cm thick on the inner section of the makatea. Other palaeosols have not been found in the makatea limestones.

According to Wood and Hay (1970, 34) the makatea limestones at Taunganui overlie 'a foot or two' of sticky yellow clay, over deep-red volcanic clay. If these clays result from subaerial weathering of the volcanics, then relative subsidence followed by reef upgrowth is indicated.

The surface of the makatea is deeply dissected, taking the form of a joint-controlled labyrinthine karst. Individual karst pinnacles and towers range in height from 3.0 to 4.5 m but locally (e.g. profile H) may exceed 6 m. There is also substantial internal limestone corrosion. We have, for example, surveyed one sinkhole which descends 22.5 m from the pinnacles on the makatea surface, the lower 11 m being a vertical fall to a freshwater pool. Caves in the makatea were first described by Williams (1838). Woodroffe visited Anetaketake cave, 500 m long, which may have been the one described by Williams. Its floor is uneven, with no evidence of either wave-cut features or changed base levels. The cave extends below the present water-level and there are pools of standing water. There are impressive stalactite, stalagmite and flowstone deposits, with sequences of rimmed terracettes. Marshall (1930) suggested that the horizontal caves may have been original reef passages, but there seems to be no evidence of this: they are clearly predominantly solutional. Some of these caves have been used as burial sites, as described by Trotter (1974).

Much of the makatea surface is irregularly covered with red clays, 'especially on the inland side' (Marshall 1930, 55). This material is clearly colluvial, derived by downslope transportation of weathered material from the volcanics, and as at Mangaia (Stoddart et al. 1985, 126) may in places predate the solutional development of the moat between volcanics and the makatea. Bizarrely, as at Mangaia (Marshall 1927, 24), Marshall (1930, 65) interpreted these clays as 'the accumulated excrement of water birds, especially of duck' (which are by no means abundant).

Limestones: Pleistocene

Marshall (1930, 56-57) himself recognised a fundamental distinction in the peripheral limestones, although he did not recognise its true significance. He found that the outer zone of limestone, 46 m wide, consisted of calcite and aragonite, whereas the limestones more than 370 m from the shore were irregularly dolomitized. Campbell (1982, 7), in a schematic section, showed the outer part of the makatea as consisting of 'coral sand and gravel' in contrast to the 'coral limestone' of the main part of the makatea.

As at Mitiaro and Mauke, these differences correspond to a transition between the main mass of makatea, of Cenozoic age, and a peripheral fringe of much younger Pleistocene limestones along the coast. The Pleistocene limestones have been studied in eight profiles around the island (figures 37 and 38). In these figures the full limestone symbol indicates limestones we consider to be Pleistocene, and the broken limestone symbol the older makatea. In general the older makatea outcrops at about 8-9 m in the south, rising to 13-14 m in the north. In several profiles the transition between older makatea and Pleistocene limestones coincides with a pronounced topographic break, at 8.6 m in profile A, 10.6 m in G, 10.1 m in H, and 12.2 m in D. In profiles B, C, E and F, however, such a break is not apparent. It would be tempting, but perhaps simplistic, to interpret the topographic break as a sea-level feature corresponding to the period of Pleistocene reef formation, especially as there is evidence from Mauke of a Pleistocene high sea level of ca 10 m (the limestones on Mitiaro are too low to reach this level). But preliminary uranium dates (to be reported elsewhere) indicate an extended period of late Pleistocene reef formation, and the stratigraphy of the Pleistocene deposits on Atiu is itself complex.

Three units can be distinguished in the Pleistocene deposits:

(a) lower unit. This is a constructional reef unit in which massive corals are dominant, with subsidiary branching corals. Interstices are filled with *Halimeda* plates and molluscan fragments. This unit is found at up to 2.65 m above sea level at Matai (profile A), and in a bench at 1.76 m at Oravaru (profile F).

(b) An intermediate unit of bedded sands, which occurs sporadically, especially at seaward locations. The presence of *Halimeda* plates up to 8 mm long suggests a beach environment. The unit is heavily cemented. At Taunganui (profile E) it contains 3 cm long vertical columnar structures which may be either root casts or burrows. In places the beds may be truncated. It is well seen at Oravaru (profile F), where it overlies *in situ* reef of the lower unit, and north of the Taunganui landing (profile E), where it overlies a boulder deposit; at both sites the sand unit is overlain by the upper unit.

(c) Upper unit. This consists of coral rubble with no corals in the position of growth within it: the only corals associated with it are superficial massive (*Porites*) or platey encrusters on the walls of grooves, and they do not form part of the unit. This may be a forereef rubble, possibly associated with the presumptive 10 m sea-level.

Coastal morphology

The reef flat around Atiu is generally less than 45 m wide, but reaches a maximum of 90 m near Oravaru on the west side (profile F). The reef flat is absent for a distance of about 2 km in the Totika area in the north (profile D). Wave conditions on the flat are rough and erosion has scoured depressions in it in which large and often coalescent

microatolls grow. The deepest depression measured was 66 cm below mean sea level. No emergent corals or reef flat was seen, unlike Mauke and Mitiaro, although the microatoll upper surfaces are dead. Marshall (1930) thought the reef flat a constructional rather than an erosional feature, because of what he judged to be the small amount of erosion of the limestones where the flat was absent, but this is unlikely. At Totika (profile D), where the reef flat is absent, there is a well developed surf platform (Focke 1978) of calcareous red algae standing ca 1 m above sea level. This effectively protects the cliff behind it, which is, nevertheless, deeply notched (figures 48-51). The notch, related to present sea-level, is up to 2-3 m in vertical amplitude. On the top of the cliff there is a solutional topography of hummocks and depressions (figure 42) and blind gullies, at an elevation of 6.5 m. Offshore there are well-developed contemporary groove-and-spur features on the reef edge.

The seaward cliffs cut in the limestones are higher in the northeast (more than 10 m) and lowest in the southwest (3-6 m), corresponding to differences in height of the limestones themselves. Along the northwest coast between Totika and Teanapuku (profile C) they reach more than 20 m in height, with a maximum of about 26 m.

Fossil groove and spur features are found in many localities. At Taunganui (profile E) they are 6-8 m wide and several metres deep. As at Mangaia they may be arched over at their seaward ends. Encrustations of platey corals are common on their walls.

Holocene coastal features

Intermittent benches and raised notches on the seaward cliffs may provide evidence of recent high stands of the sea (figures 45 and 46). There are cliff-foot benches at 2.78 m on profile A, a bench (with associated notch) at a 1.8 m on profile F, at 1.78 m on profile G, and at 3.1 m on profile H. In several places the benches are being eroded and merging into the reef flat. There are raised notches in the cliff face above present intertidal levels, for example at 3.27 m on profile C and at 2.8, 3.0 and 3.6 m on profile H, giving complex profiles (figures 44 and 45) indicative of falling sea-levels (Pirazzoli 1986, 373-375). The dominant levels for benches and raised notches are 1.7-1.8 m and 2.8-3.2 m above present sea level. There is some indication of possible older features at ca 6 m in profiles A, B, E, G and H.

There are, however, no extensive areas of emerged reef-flat on Atiu, as there are on Mauke and especially Mitiaro.

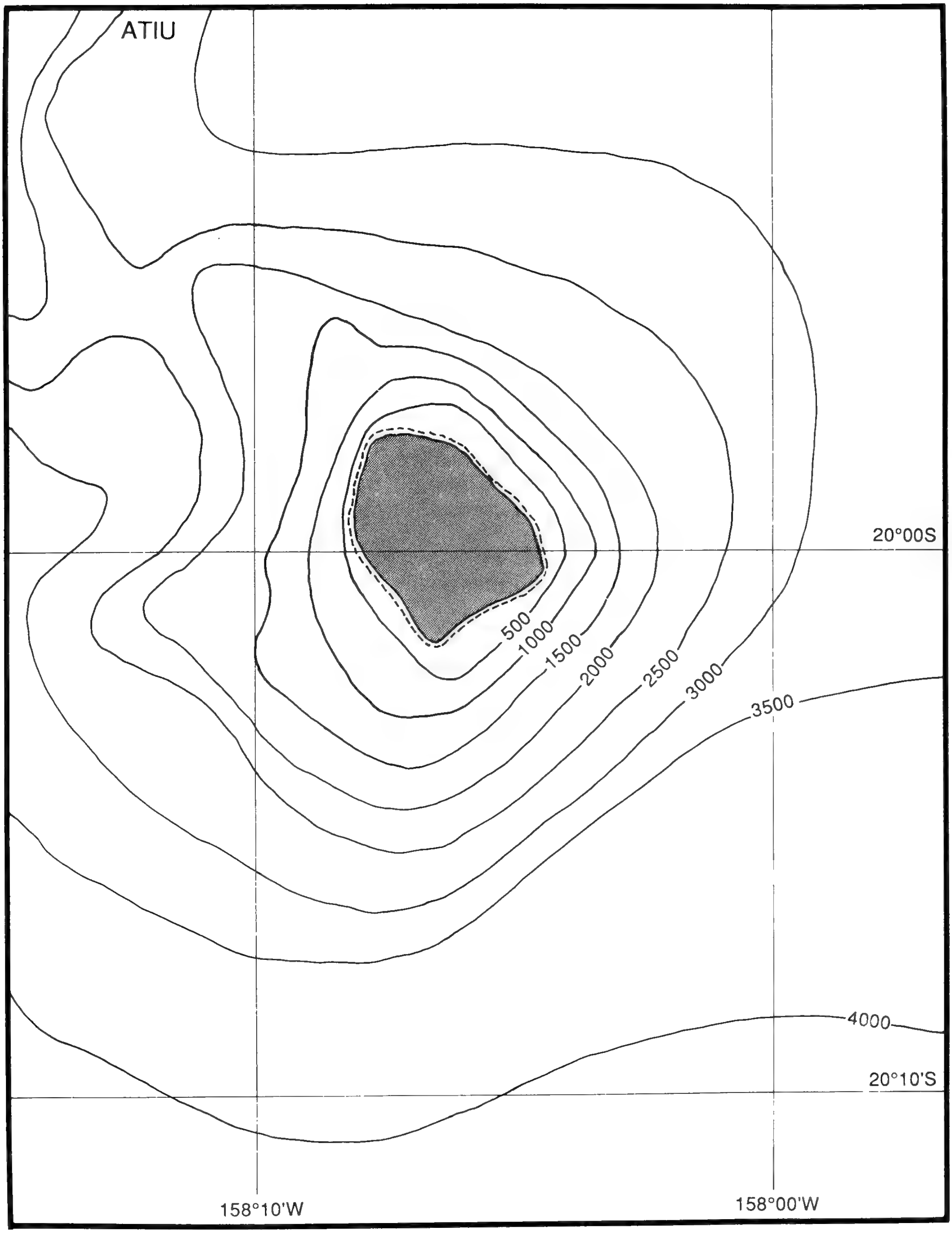


Figure 35. Bathymetry of Atiu (after Summerhayes and Kibblewhite 1968)

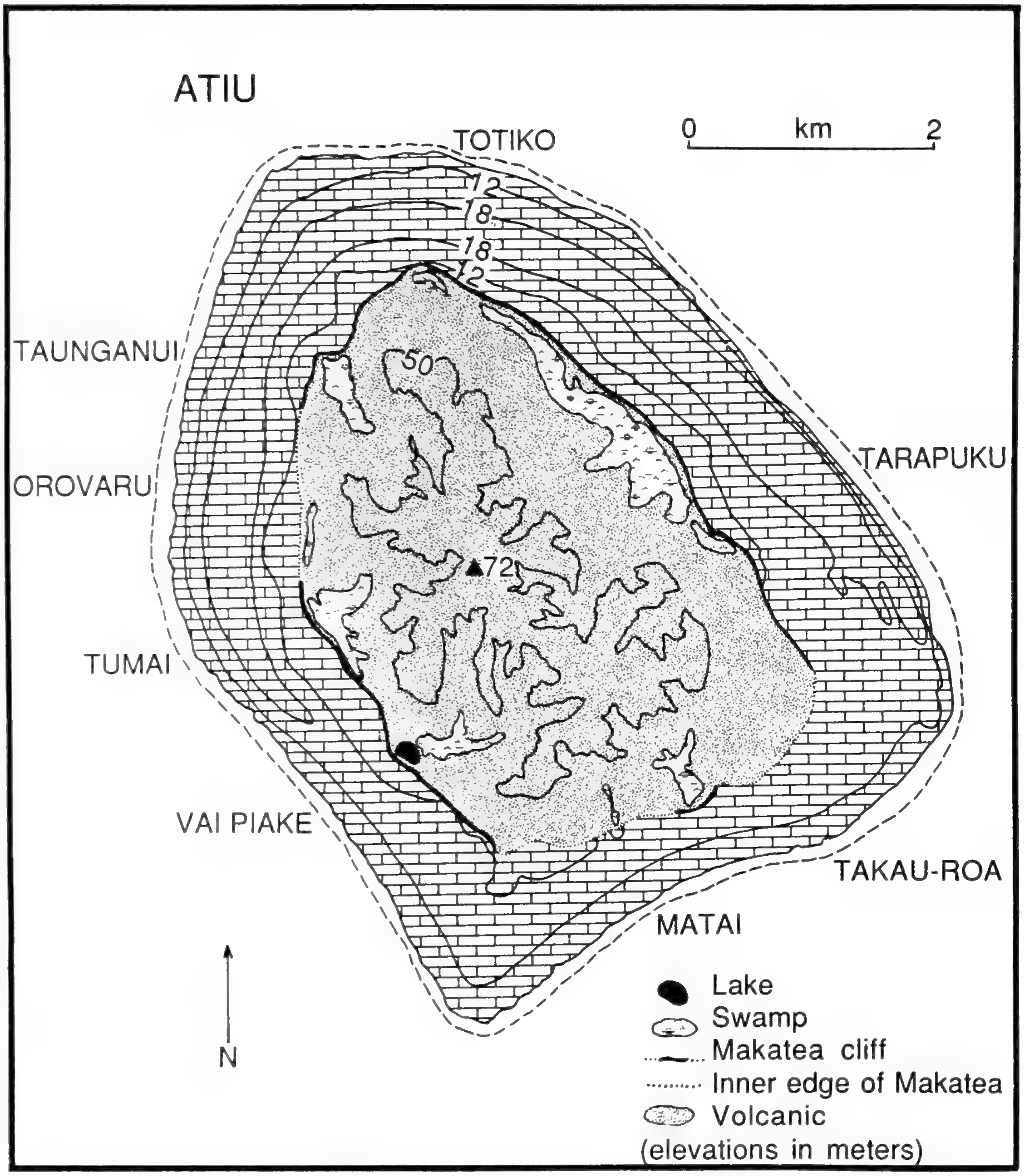


Figure 36. Geology of Atiu

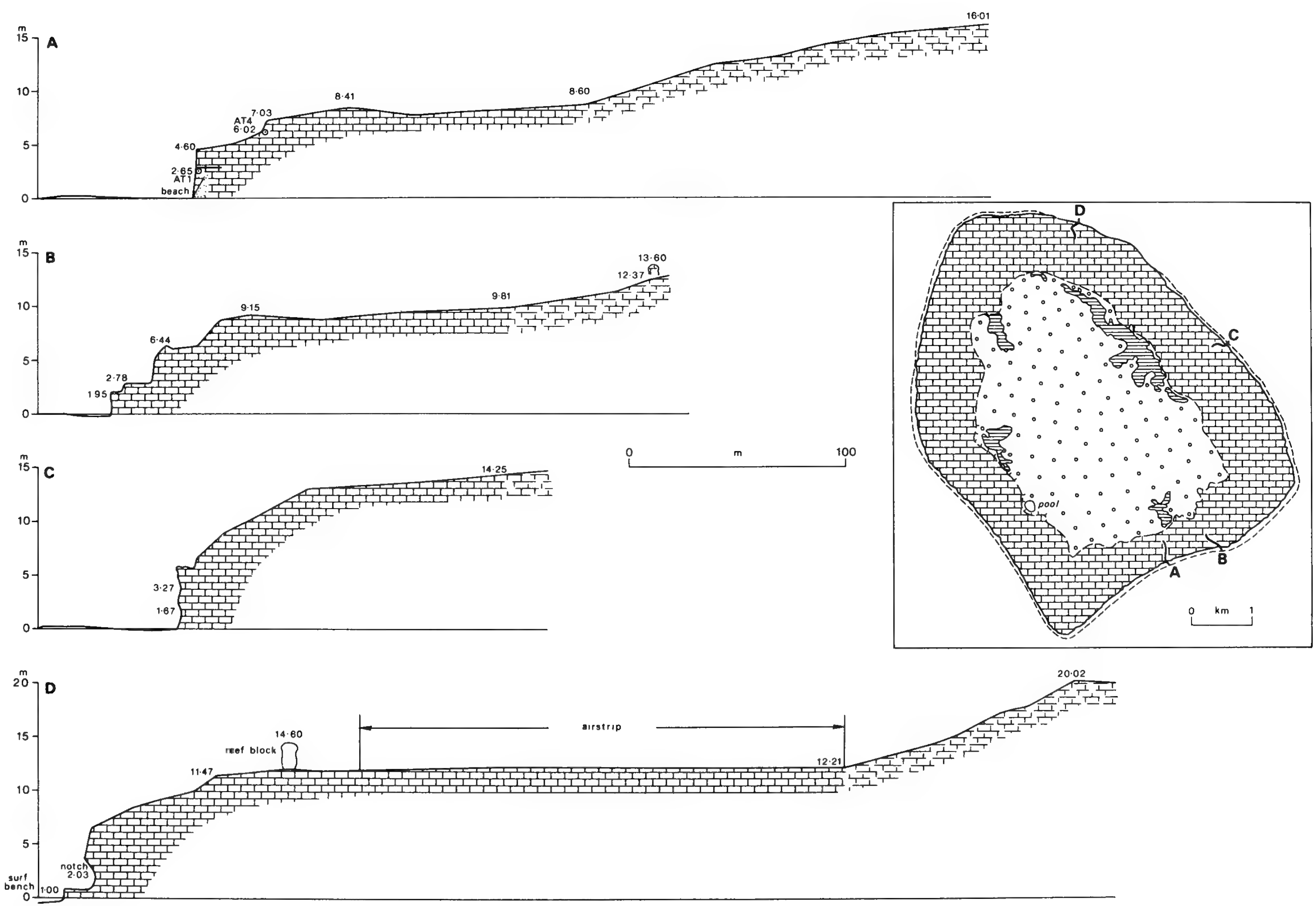


Figure 37. Atiu: topographic profiles A, B, C and D

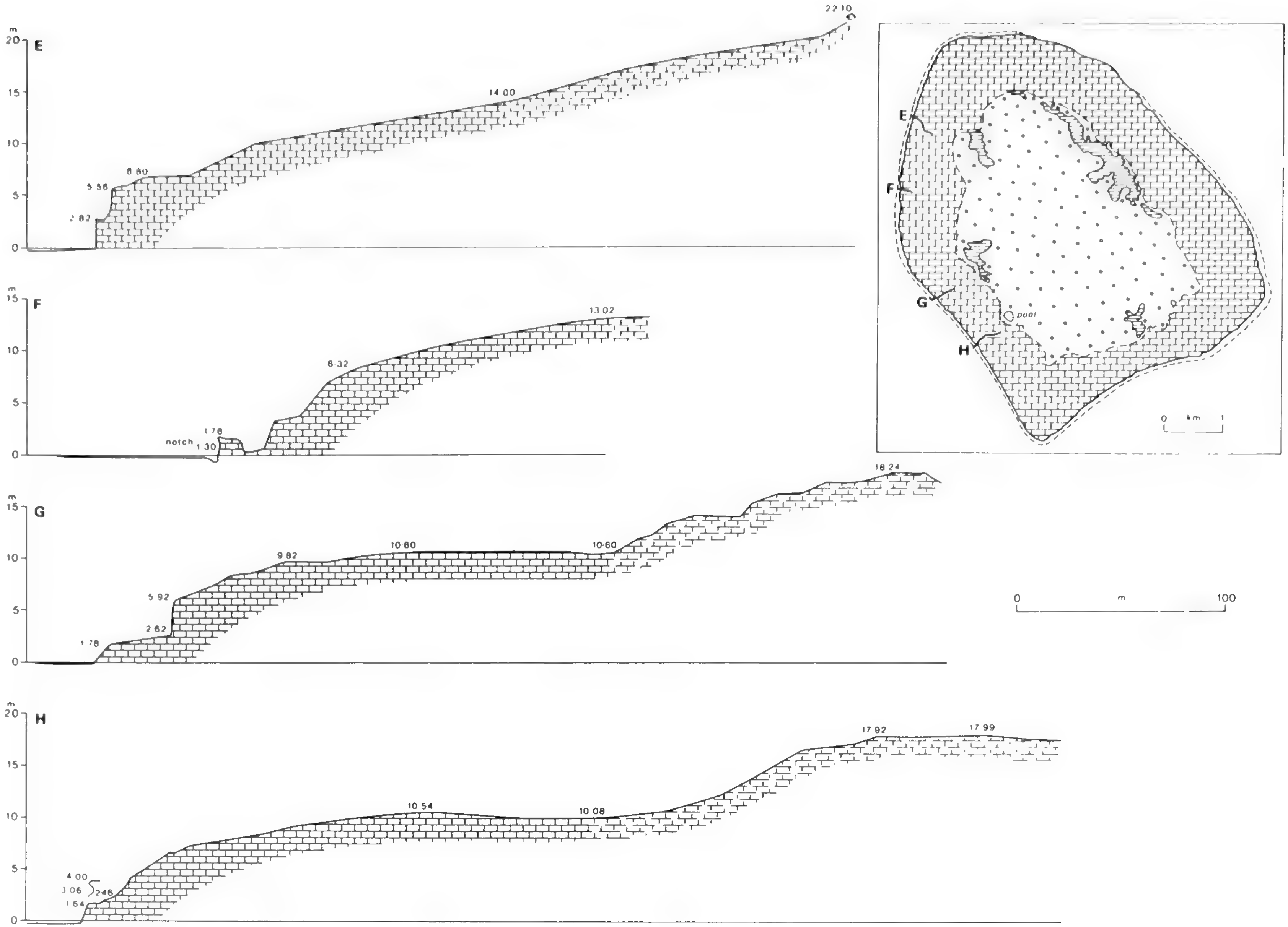


Figure 38. Atiu: topographic profiles E, F, G and H

Figure 39.   Bevelled upper surface of the central volcanics on Atiu

Figure 40.   Lake Tiriroto on the southwest side of Atiu

Figure 41. Basally notched cliffs on the inner side of the makatea near Lake Tiriroto, Atiu

Figure 42. Mammillated surface of limestones inland from the cliff edge at Totika (profile D), Atiu

Figure 43. Makatea surface at Orovaru, Atiu

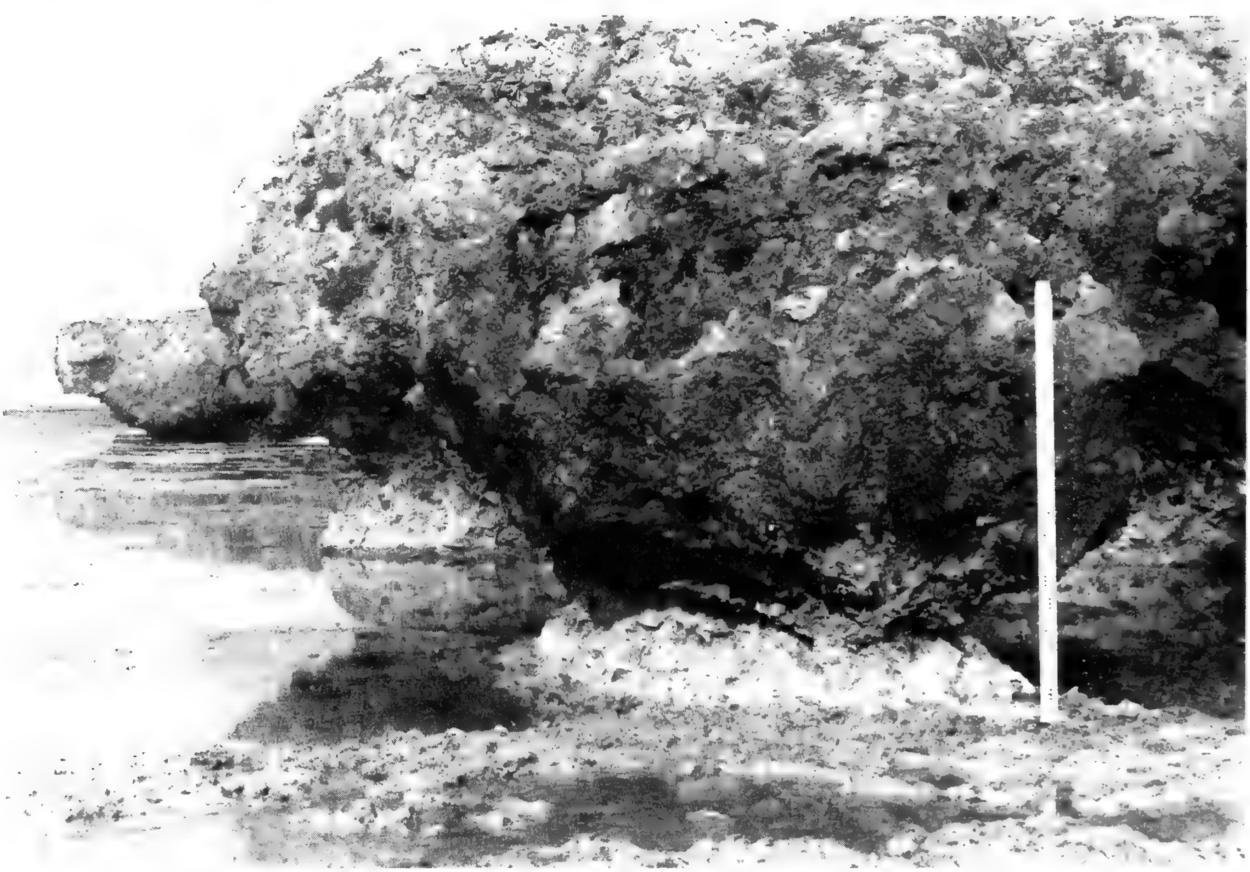


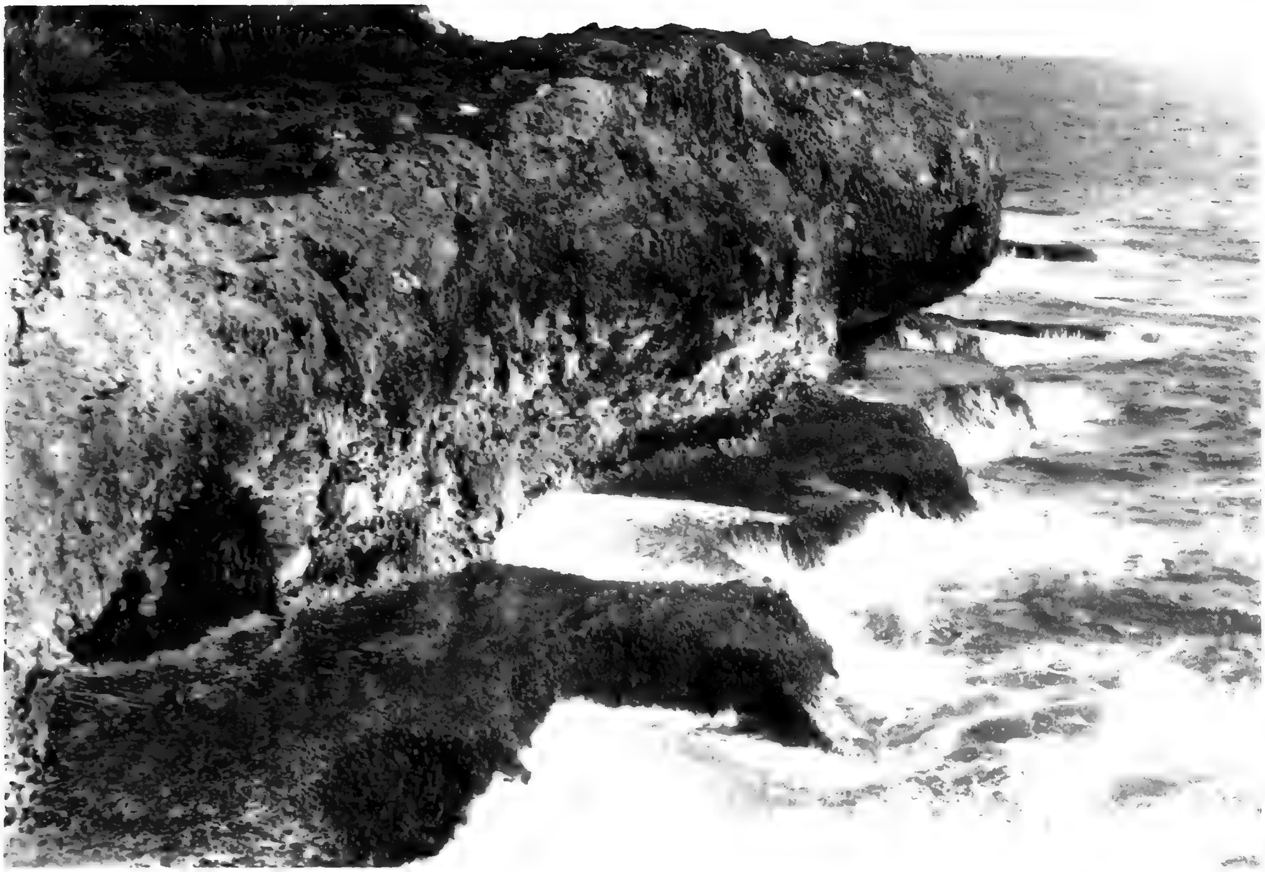
Figure 44. Basally notched coastal cliffs, southwest coast of Atiu

Figure 45. Double-notched cliffs at Teanapuka, east coast of Atiu

Figure 46. Basally-buttressed cliffs at Vaipiake, Atiu

Figure 47. Aerial view of basally notched cliffs at Totika, Atiu

Figure 48. Surf bench at Totika, Atiu



Figures 49 and 50. Surf bench at Totika, Atiu

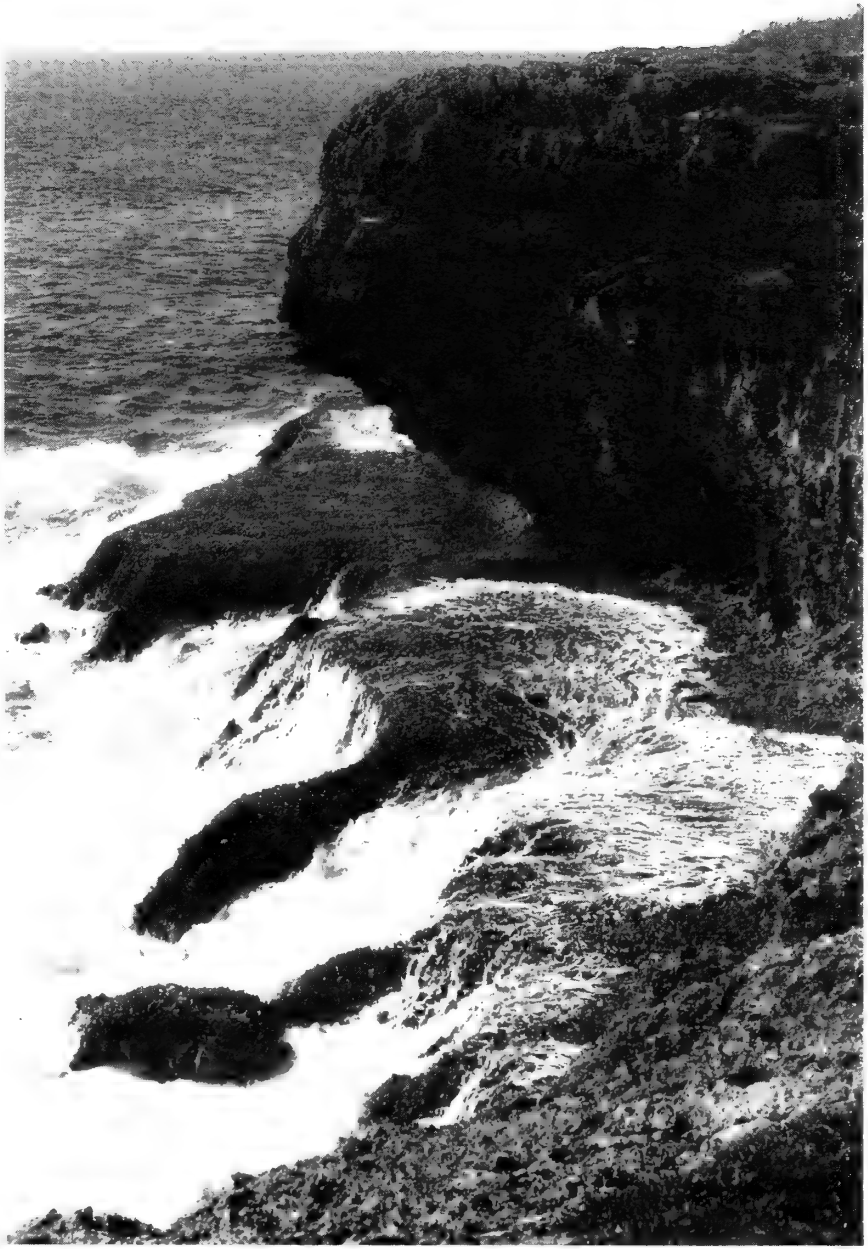


Figure 51. Surf bench at Totika, Atiu

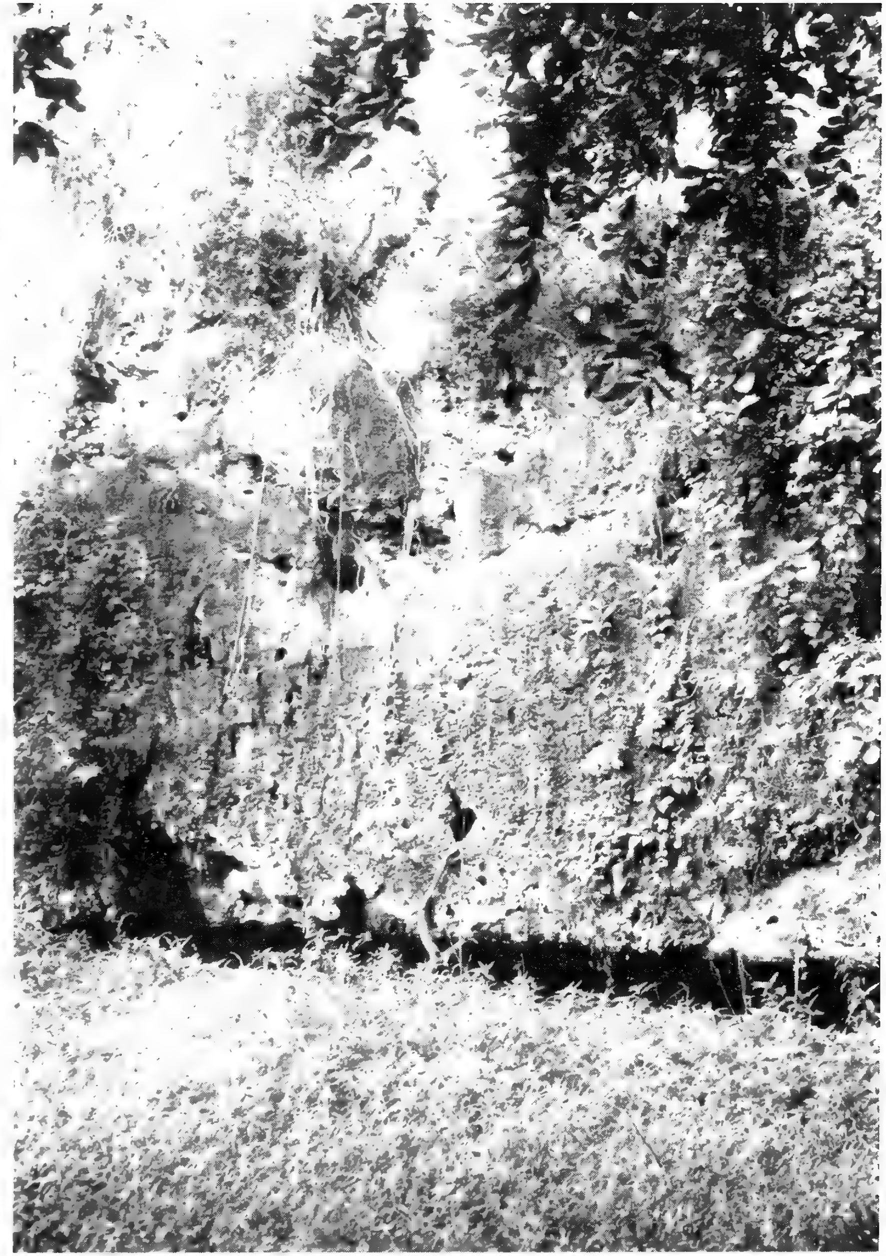


Figure 52. Basal notch in inner makatea cliff on the west coast of Atiu

DISCUSSION

In this section we summarise the salient features of the geomorphology of Mitiaro, Mauke and Atiu, and make some comparisons with other islands in the southern Cooks, notably Mangaia and Aitutaki.

Volcanics

We have established the maximum elevation of the volcanics on Mitiaro as 8.9 m (previous estimates 6.0-12.2 m) and on Mauke as 24.4 m (previous estimates 25-30 m). The maximum elevation on Atiu from the Otago topographic map is 71 m. These heights compare with 124 m for Aitutaki and 169 m for Mangaia. Mitiaro is the only island in the southern Cooks on which the maximum elevation of the volcanics is less (by 2 m) than the maximum elevation of the makatea, and it seems likely that in this case the makatea formerly completely covered the volcanics which have been unroofed by karst erosion.

The upper surface of the volcanics is conspicuously horizontally bevelled at both Mauke (at 20-24 m) and at Atiu (at ca 65-70 m). The higher parts of both Aitutaki and Mangaia are likewise bevelled, at ca 75 m and 165 m respectively. Previous workers have attributed these bevels to marine erosion and it is difficult to think of any other reasons for such smooth truncation of previously conical topography. Indeed, if one extrapolates the regular submarine volcanic topography of many of the Cook Islands, to which Robertson and Kibblewhite (1966) fitted the expression $y = y_0 e^{-0.10x}$ (where y is depth at distance x from shore and y is mean depth of the surrounding ocean floor, 4.6 km), it is evident that very substantial truncation has taken place on these cones.

Mauke and Mitiaro are too low to display benches or terraces below the summit bevel. Conspicuous terraces have been described for Atiu at 45, 20 and 7-15 m (Campbell et al. 1978); Schofield (1967, 119) gives comparable terrace heights of 21 and 12 m, and adds a further level at 4.6 m. No similar terraces have been described from Mangaia, but at Aitutaki Wood and Hay (1970) refer to wave-cut terraces at 76, 18-21 and 12 m, and Lambeck (1981, 484) mentions 'several marine terraces up to 120 m'. The 76 m level is close to the summit level of Atiu. The Aitutaki 18-21 m level (if real and significant) corresponds altitudinally with the summit level at Mauke (20-24 m) and the 20-21 m terrace at Atiu. The Aitutaki 12 m terrace (again, if real and significant) lies above the Mitiaro summit level (8-9 m), but corresponds to the terrace described by Schofield at 12 m and by Campbell et al. at 7-15 m on Atiu, and it is also close to the maximum height of late Pleistocene shorelines on Mauke, Mitiaro and Atiu. But it should be emphasised that none of these features in the southern Cooks has been rigorously mapped or levelled, and that there is no direct evidence of their marine origin at all.

Makatea

The maximum elevation of Cenozoic limestones is shown by our surveys to be 10.9 m on Mitiaro and 14.7 m on Mauke. The Otago topographic map gives the maximum height on Atiu as 23 m.

The upper surfaces of the makatea at Mitiaro and Mauke are broadly horizontal. The convexity of the surface in cross-profile at Atiu is indicative of considerable post-uplift

erosion, however. The horizontality at the former islands could well reflect bevelling by late Pleistocene sea levels. The degree of post-emergence modification at Atiu is unknown, but in the case of Mangaia we have argued that the development of the swamplands by limestone retreat effectively isolates the surface of the makatea from fluvial dissolution as the streams draining the central volcanics exit through the limestones close to present sea level. Thus most of the karst erosion in the makatea is internal to the limestone body and the external geometry of the makatea is relatively resistant to change (Stoddart et al. 1985, 127). Two points need to be considered at Atiu in judging the degree of modification and neither is unambiguous. The first is the unsupported statement by Jarrard and Turner (1979, 5693) that outcrops of makatea are found on the volcanic slopes of the island at an altitude of 55 m, or 32 m above the present maximum height of the makatea. If correct this would indicate a degree of erosional modification of the makatea on a scale hitherto never contemplated. We doubt this record, as we did their reference to makatea outliers at 90 m on the Mangaia volcanics (Stoddart et al. 1985, 136). Second, at both Atiu and Mangaia Wood and Hay (1970) refer to the existence of concentric structures in the makatea, evident in aerial photography, as evidence of the exposure of internal seaward-dipping depositional structures by surficial erosion. It is impossible to quantify the magnitude of this effect, however.

A more specific index of the erosional modification of the limestones is given by the presence at Atiu of colluvial weathered materials from the volcanics on the inner slopes of the makatea. There are no precise data on the distribution of this colluvium, but it can be inferred from Campbell (1978, 231) that it extends to an elevation of ca 20 m above sea level. It was presumably progressively deposited downwards as the 'moat' between the volcanics and the makatea was incised by erosion, though there is also the possibility that the swamp levels were at higher elevations during Pleistocene high stands of the sea and that some of the colluvium may be relict from that time.

A major difficulty in understanding the makatea is that the ages of the formation of the limestones as well as of their emergence is unknown. At Mangaia Marshall (1927) believed the limestones were of Oligocene and lower Miocene age, or younger. Recently Yonekura et al. (1986, 50) have inferred an age of 17 million years from foraminifera collected on the innermost upper surface of the makatea, i.e. very soon after volcanism: the K-Ar ages of Mangaia volcanics range from 16.6 to 19.4 million years, with one young date of 13 million years. Unlike Rurutu in the Austral Islands (Bardintzeff et al. 1985), however, we have seen no exposures where volcanic conglomerates occur near the base of the makatea, which would suggest the contemporaneity of initial reef growth and continuing volcanism. The volcanics on Mitiaro, Mauke and Atiu are apparently substantially younger (12.3, 6.0, and 8-10 million years, respectively). There is therefore a real possibility that the makatea units on the different islands are of different ages and hence their morphologies cannot be directly compared. Marshall (1930) himself believed the Atiu limestones to be early Pliocene and later.

Whatever the age of the limestones, however, it appears reasonable to follow McNutt and Menard (1978) in explaining their emergence by lithospheric flexure consequent on loading by subsequent volcanicity. Two points might be made about their analysis, however. The first is that their calculations of net uplift incorporate loading by the three volcanoes of Rarotonga, Aitutaki and Manuae, of which only the first is known to postdate the formation of Mitiaro, Mauke and Atiu. The second is that their calculations depend on the independent response of each of the volcanoes, and it is by no means clear that this condition would be met with such closely associated cones as the three under discussion. Nevertheless, it is pertinent to use our new elevation data from the makatea to re-examine the goodness of fit of the McNutt and Menard model (Spencer et al. 1987). These data are summarised here in Table 4.

Table 4. Island uplift and lithospheric flexure in the southern Cooks

A Island	B Distance from Rarotonga km	C Maximum elevation of volcanics m *	D Maximum elevation of makatea m *	E Actual uplift according to McNutt & Menard, m **	F Predicted net uplift through loading by Rarotonga, Aitutaki and Manuae, m **	G Predicted uplift through loading by Rarotonga only, m **	H Goodness-of-fit of model (G - D)
MAUKE	281	24.4	14.7	30.0	28.8	17.0	+ 2.3
MITIARO	264	8.9	10.9	27.0	27.4	25.0	+14.1
ATIU	222	71.0	22.1	20.0	17.7	48.0	+25.9
MANGAIA	205	169.0	73.0	70.0	50.5	51.0	-22.0

* This paper

** McNutt and Menard (1978)

Pleistocene events

The maximum elevation of Pleistocene features on the seaward side of the makatea was found to be 7.8 m on Mitiaro, 12.7 m on Mauke, and 12.2 m on Atiu: Mitiaro is anomalously low simply because the makatea on which the Pleistocene reefs formed does not itself rise above 10.9 m. In consequence, whereas on Mauke and Atiu the Pleistocene deposits are banked against the seaward edge of the makatea, on Mitiaro they are spread across its upper-surface in many areas. There are no Pleistocene deposits on Aitutaki; on Mangaia there is a prominent shoreline at 20 m. Prominent stratigraphic discontinuities are found within the Pleistocene at 4.1-6.0 m on Mitiaro, 1.5-2.75 m on Mauke, and 1.75-2.65 m on Atiu. These themselves indicate a fairly complex late Pleistocene history, and this is supported by unpublished uranium-series dates (Woodroffe *et al.*, in preparation), in contrast to Mangaia where the uranium-series dates tie the deposits closely to last interglacial times (Veeh 1966; Spencer et al. 1988).

The floors of raised groove-and-spur features associated with late Pleistocene reef deposits rise inland from the coast to maximum heights of 5.7 m on Mitiaro, 7.5 m on Mauke, and 6.5 m on Atiu. On Mangaia similar features rise to 11 m.

Holocene features

Raised notches and occasional cliff-foot benches also record sea-level fluctuations over a shorter time scale. Notches reach 2.3 m on Mitiaro, 0.6-1.5 and 5.5-6.5 m on Mauke, and 2.8-3.6 m on Atiu. Benches on Mauke reach 2.7 m and on Atiu 1.8-3.1 m. Benches and associated notches are found on Atiu at 1.7-1.8, 2.8-3.2, and possibly 6 m.

Anomalously high sectors of reef flat of possibly Holocene age are found at 1.23 m on Mitiaro. These may correlate with the notches and benches in the height range 2.3-3.6 m.

Apparently anomalously high beachrock is found up to 1.96 m on Mitiaro.

These features taken together resemble the emerged benches, high notches at 2-3 m, uplifted microatolls at 0.95-1.5 m, and raised and eroding reef flats described by Yonekura et al. (1986, 1988) on the northwest coast of Mangaia, except that the Mitiaro, Mauke and Atiu elevations are somewhat greater than those on Mangaia. Yonekura et al. (1986, 1988) show that the features on Mangaia all date from a high stand of the sea at 1.0-1.7 m above present in the interval 5000-ca 3150 years B.P., after which sea level fell to its present level or less, when contemporary reef flats and notches began developing. These differences may result from flexural control.

Modern coastal features

Perched beaches are extensive on the cliff tops of Mitiaro and Mauke, where they reach heights of 10.9 and 12.7 m respectively; the cliffs of Atiu are too high and steep for perched beach formation.

Storm-thrown reef blocks are common on the cliff tops of both Mitiaro and Mauke, at heights of 4.9-6.8 m on the former and 6.9-9.2 m on the latter, at distances of 9-200 m from the cliff edge.

ACKNOWLEDGEMENTS

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ATOLL RESEARCH BULLETIN

NO. 342

NOTES ON THE BIRDS OF KWAJALEIN ATOLL, MARSHALL ISLANDS

BY

R. B. CLAPP

ISSUED BY

NATIONAL MUSEUM OF NATURAL HISTORY

SMITHSONIAN INSTITUTION

WASHINGTON, D.C., U.S.A.

SEPTEMBER 1990

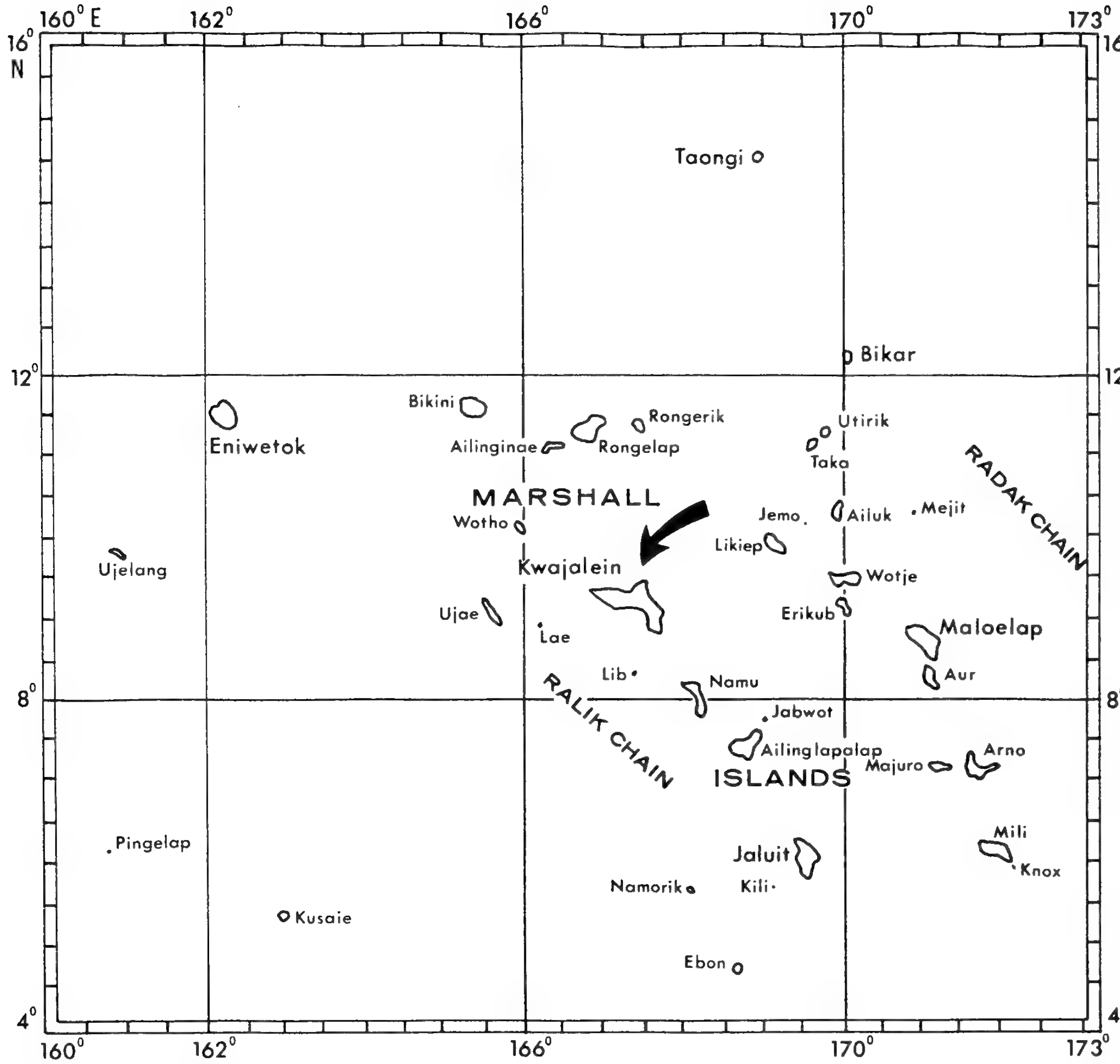

Figure 1. Location of Kwajalein Atoll in the Marshall Islands.

NOTES ON THE BIRDS OF KWAJALEIN ATOLL, MARSHALL ISLANDS

BY

R. B. CLAPP

Introduction

Kwajalein is a crescent-shaped atoll that lies between 09°25' and 08°40'N and between 166°50' and 167°45'E, near the center of the western (Ralik) chain of the Marshall Islands (Figure 1). Composed of more than 90 islets, largely uninhabited, Kwajalein Atoll extends about 75 miles from southeast to northwest. It has a land area of about 6 square miles (3,854 acres) (Global Associates 1987), an increase of about 263 acres over the original area that was brought about by filling of land on Kwajalein, Roi-Namur, and Meck Islands.

As of June 1987, the population of the atoll was about 12,200 and composed of about 9,560 Marshallese and 2,639 non-indigenous persons affiliated with the U.S. Army Kwajalein Atoll (USAKA) facility. The three islands of Ebeye (8,600; mostly Marshallese), Kwajalein (2,390) and Roi-Namur (249) hold over 90% of the population (Global Associates 1987).

During March 1988, I made ornithological observations on ten islands (Figure 2). Part of a survey requested by the U. S. Army Corps of Engineers, the observations helped determine the terrestrial wildlife resources of the atoll as baseline data for an environmental impact statement. Derral Herbst, a botanist with the U. S. Fish and Wildlife Service, also participated in the survey.

We lived on Kwajalein Island, and on a typical day we flew to one of the outer islands by helicopter at about 0700 and returned between 1400 and 1630 (Table 1). Most of the islands surveyed were small, 40 acres or less, and I could easily walk their perimeters and much of the interior in a few hours. A bicycle made surveying the larger islands of Roi-Namur and Kwajalein much easier. I counted birds and noted their behavior, stage of nesting, location, and habitats. I also casually observed other terrestrial vertebrates but did not attempt a comprehensive survey.

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Table 1. Itinerary of ornithological survey conducted on Kwajalein Atoll in March 1988.

Date		Depart Kwajalein Island	Time Spent Surveying Island	Island Surveyed	Arrive Kwajalein Island
8th	Tues.		1530-1800	Kwajalein	1100
9th	Wed.	0700	0715-0920	Ennylabegan (Carlos)	0925
10th	Thur.	0710	0720-1455	Ennylageban	1505
11th	Fri.	0738	0805-1542	Legan	1556
12th	Sat.-	1140	1200-	Roi-Namur	
13th	Sun.		-1223		1245
14th	Mon.	0733	0750-1601	Illeginni	1621
15th	Tues.	0825	0905-1545	Gagan	1615
16th	Wed.	0745	0805-1505	Gellinam	1556
17th	Thur.	0742	0802-1442	Omelek	1502
18th	Fri.	0702	0717-1252	Eniwetak	1305
19th	Sat.-			Kwajalein	
20th	Sun.				
21st	Mon.	0704	0721-1445	Meck	1510
22nd	Tues.	0915	0937-1603	Illeginni Island	1623
23rd	Wed.	0706	0712-1448	Ennylabegan	1455
24th	Thur.	0729	0742-1517	Legan	1529
25th	Fri.	0740	0812-1530	Gagan	1557
26th	Sat.-	0704	0723-	Roi-Namur	
27th	Sun.		-1223		1243
28th	Mon.-			Kwajalein	
29th	Tues.				
30th	Wed.	1034			

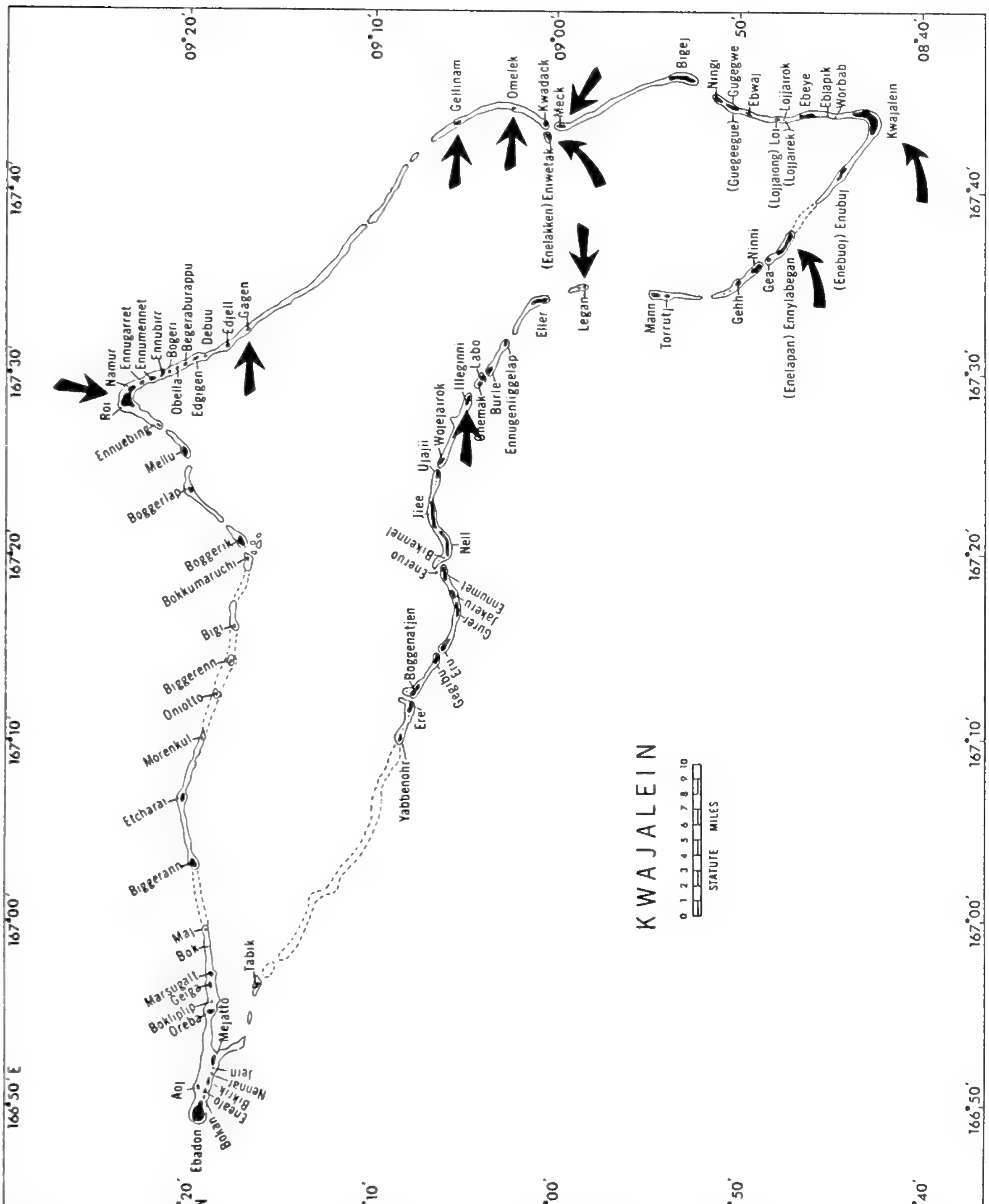

Figure 2. Kwajalein Atoll. Arrows indicate islands surveyed.

The combined area of the islands surveyed in March was 1,408 acres, a little more than a third of the total land area. Brief descriptions of the islands and their habitats are given below.

Ennylabagen, or Carlos covers 124 acres, lies 8 miles northwest of Kwajalein, and orients generally northwest-southeast along the atoll rim. One village occupies the northern end, and another is situated in the south-central portion (Figure 3). The central portion of the island contains various facilities, a helipad, and a variety of open antennae fields (Figure 4) interspersed with scrubby areas and low forest. The northern and southern ends are more heavily forested, and the southern end provides the best habitat for birds. A thick stand of Pemphis trees grows along the southeastern shore; Cocos and Pisonia trees dominate the rest of the area. A trail follows the outer perimeter of the island's southern (Figure 5).

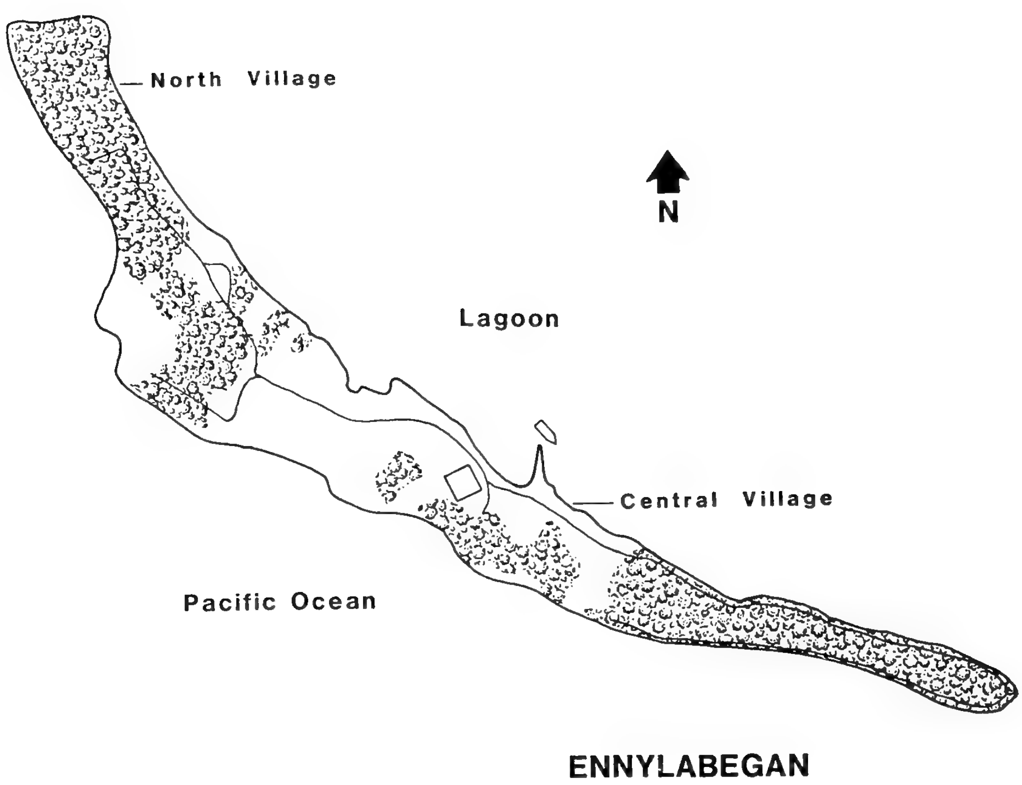

Figure 3. Ennylabagen Island. Principal area of shorebird concentration is WNW of the helipad.

Figure 4. Looking W at large antenna field near helipad on Ennylabagen, 10 March 1988. (All photographs, unless otherwise stated, were taken by the author in March 1988).

Figure 5. Trail through southeastern forest on Ennylabagen. Stand of _Pemphis_ to right.

Western (ocean) shores are largely rubble with some pronounced rock ledges near the northwest point. Eastern (lagoon) shores are more sandy, but their location opposite Ebeye and Kwajalein has led to much accumulation of trash and debris.

Legan, (18 acres), lies north of Ennylabagen on the atoll's western rim about halfway between Ennylabagen and Illeginni. It is hook shaped with the point running northeast from the south end (Figure 6). The helipad and other facilities are on the southern portion of the hook and comprise about 20% of the island's area. About 70% is forested (Figure 7) with the remainder being two interior pools oriented north-south in the island's midsection (Figure 8). Pemphis, interlaced with Cassytha vines, grows so densely around the pools that access is difficult. At the larger pool's northern end open Cocos permits a fairly easy approach. The perimeter is largely coral rubble with than on the western side forming a ridge about 10 feet higher than the interior. The only sandy beaches are on the east-central portion of the island. The lagoon area of this shore and north of the hook is very shallow, and a large, sandy expanse is exposed at low tide.

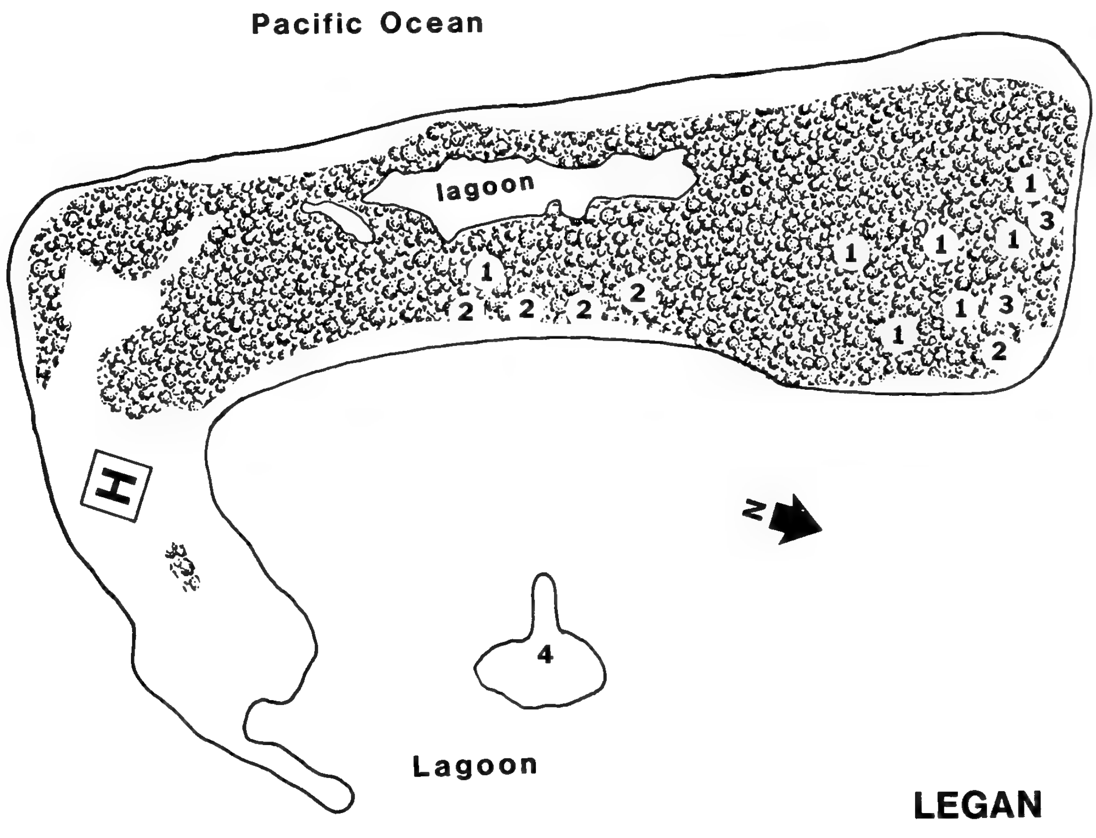

Figure 6. Legan Island. (1) Nesting area of White Terns; (2) nesting area of Brown Noddies; (3) nesting area of Black Noddies; (4) roosting area of Crested and Black-naped Terns.

Figure 7. Looking south at forest on northern end of Legan from point at northeastern corner marked 2 in Figure 6.

Figure 8. Northern (larger) interior pool on Legan from the north. Cassytha entangled vegetation in background.

Illeginni is 31 acres and lies on the southwestern rim. Also hook-shaped, it lies with its long axis essentially from west-northwest to east-southeast with the hook pointing north into the lagoon (Figure 9). A helipad at the west end is connected by a road down the center of the island to the facilities and harbor at the east end (Figure 10). The central portion of the east end has been artificially elevated to about 40 feet. Perhaps 70% of the island has been cleared, but at least some of this area, particularly along the central road, is covered by rank undergrowth. The principal forest stands remaining are on the west end, fringing the east end, and on either side of the central road on the island's southern half. The shoreline of Illeginni is mostly medium to coarse coral rubble with occasional patches of sand. The water along the southern third of the western shore is very shallow and usually provides exposed areas and tide-pools where herons and shorebirds forage. North of Illeginni is an isolated smaller island (Figure 11) of perhaps one acre that is scantily vegetated and which can be reached dryshod at low tide. It has broad, sandy beaches from the south along the lagoon side to the north spit and a rough rubble-lined ocean shore.

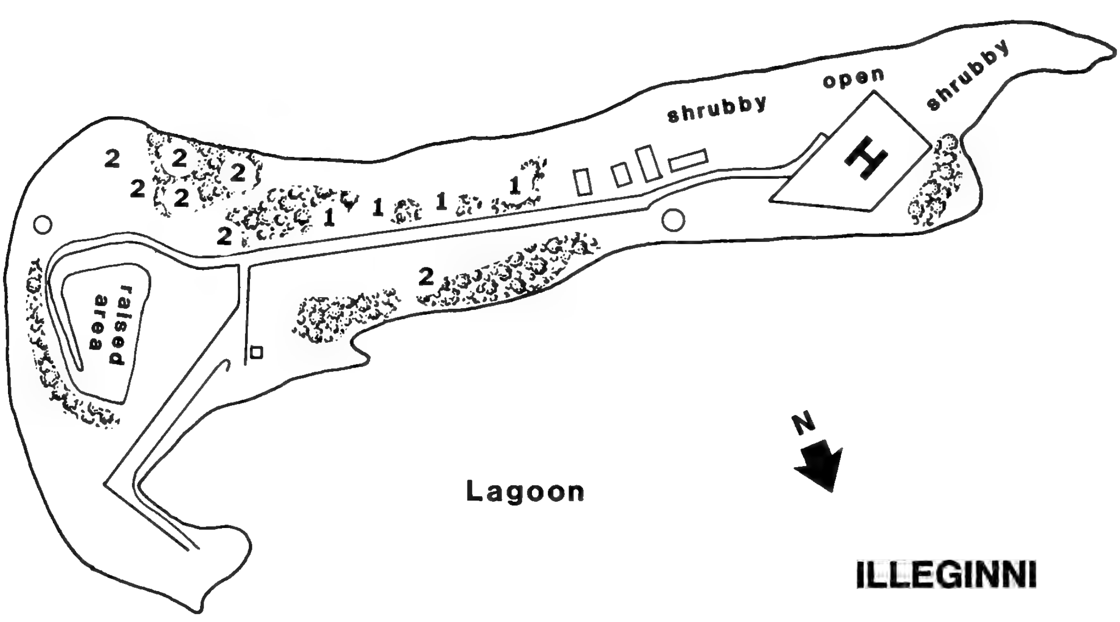

Figure 9. Illeginni Island. (1) Nesting area of Brown Noddies; (2) nesting area of Black Noddies.

Figure 10. Illeginni Island looking west-northwest from the elevated area on the east end. Coconuts to the left of the central road are the principal nesting area of Brown Noddies.

Figure 11. Illiginni Island, looking north toward isolated northern island.

Roi-Namur covers 398 acres and lies about 50 miles north-northeast of Kwajalein from which it may be reached by daily flights. It was formed from the three islands of Roi, Enedrikdrik, and Namur. The western portion (Roi) contains an airstrip, residential and work areas, and a golf course and is largely open with only scattered stands of shrubs and trees (Figure 12). The south tip of Roi has an extended sandy point that is attractive to shorebirds and resting terns. The eastern portion (Namur) has several large facilities and a large inlet (Figure 13). This portion is much less developed and contains more forest and scrubby area. Docking facilities are located on the southern (lagoon) shore, and sandy beaches are found on southern, western, and northern shores. The eastern and north-eastern shores of Namur are rocky, and at low tide provide attractive foraging habitat for shorebirds.

Gagan is the last island in a string of about a dozen running southeast from Roi-Namur. It is a 6-acre oblong that runs north-south, and about half the island has been cleared. A helipad, buildings, and a dock are found on the southern third of the island; and the center of the island has been cleared to the north tip (Figures 14, 15). A small grove runs east-west across the south end (Figure 16) and shrubs and trees line the shores of the northern two-thirds of the island. Those on the western (lagoon) when I visited and many lacked leaves. The eastern and southern shores are rough rubble, and the western shore is sandy. A small sand-spit

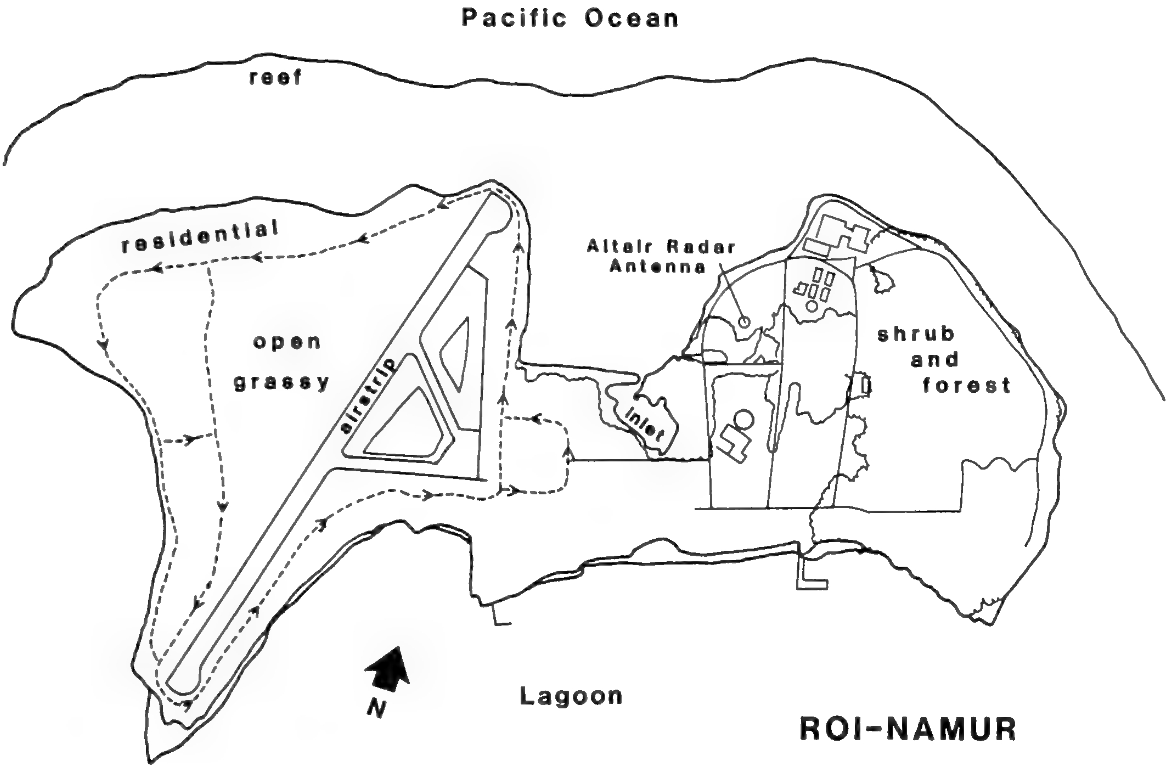

Figure 12. Roi-Namur Island. Dotted lines show route of shorebird surveys.

extends off the north tip of the island (Figure 17), and a much larger one is south of the piers at the southwestern corner. Areas to the north and along the lagoon shore are shallow and at low tide expose rocks that are used by roosting terns.

Gellinam, Omelek, Eniwetak, and Meck are all on the atoll's southeastern rim and about due north of Kwajalein. Five-acre Gellinam is long and narrow and runs roughly north-northeast to south - southwest (Figure 18) Little native vegetation remains; most of the island has been cleared for the helipad and structures on the southern three-quarters of the island. A *Pisonia* forest running across the northern portion contains a substantial Black Noddy (*Anous minutus*) colony. Sandspits extend to the north and south and a pile of large rock blocks at the north end (Figure 19) provides an attractive roosting area for Black-naped Terns (*Sterna sumatrana*).

Omelek Island is small (8 acres) and roughly triangular with points to the northeast, west, and south (Figure 20). Sandspits lie off the northeast and south points with some rough coral rubble along the north side. About 80% of the island has been cleared for the

Figure 13. Roi-Namur Island. Inlet from ocean on Namur. Sandy area to left is favored by Wandering Tattlers for roosting.

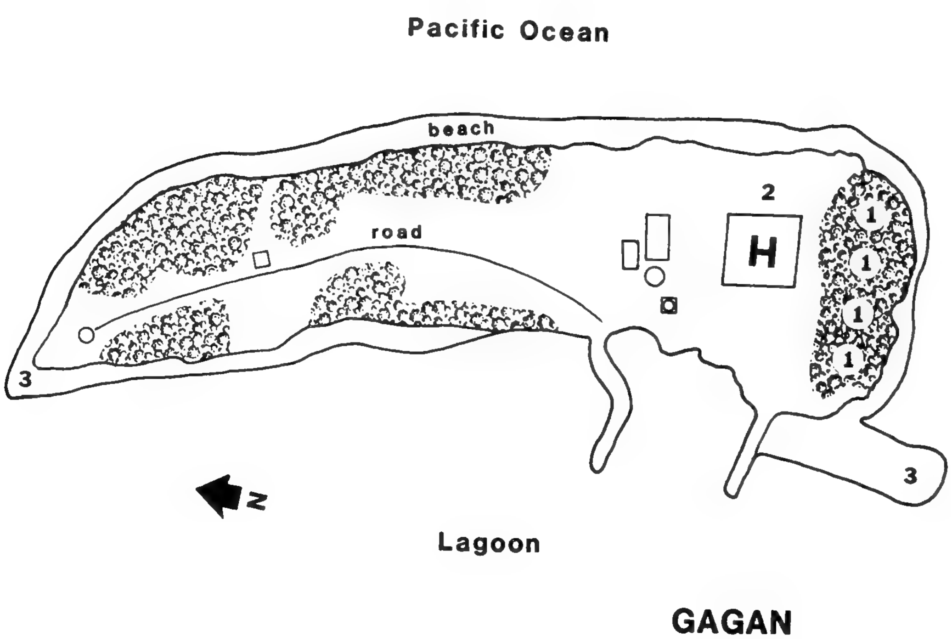

Figure 14. Gagan Island. (1) Presumed nesting area of White Terns; (2) nesting area of Black-naped Terns in 1979; (3) principal roosting area of Black-naped Terns.

Figure 15. Gagan Island. Looking north from facilities at the south end of the island.

Figure 16. Small grove of open Pisonia at the south end of Gagan Island.

Figure 17. Rubble spit at the north end of Gagan Island.

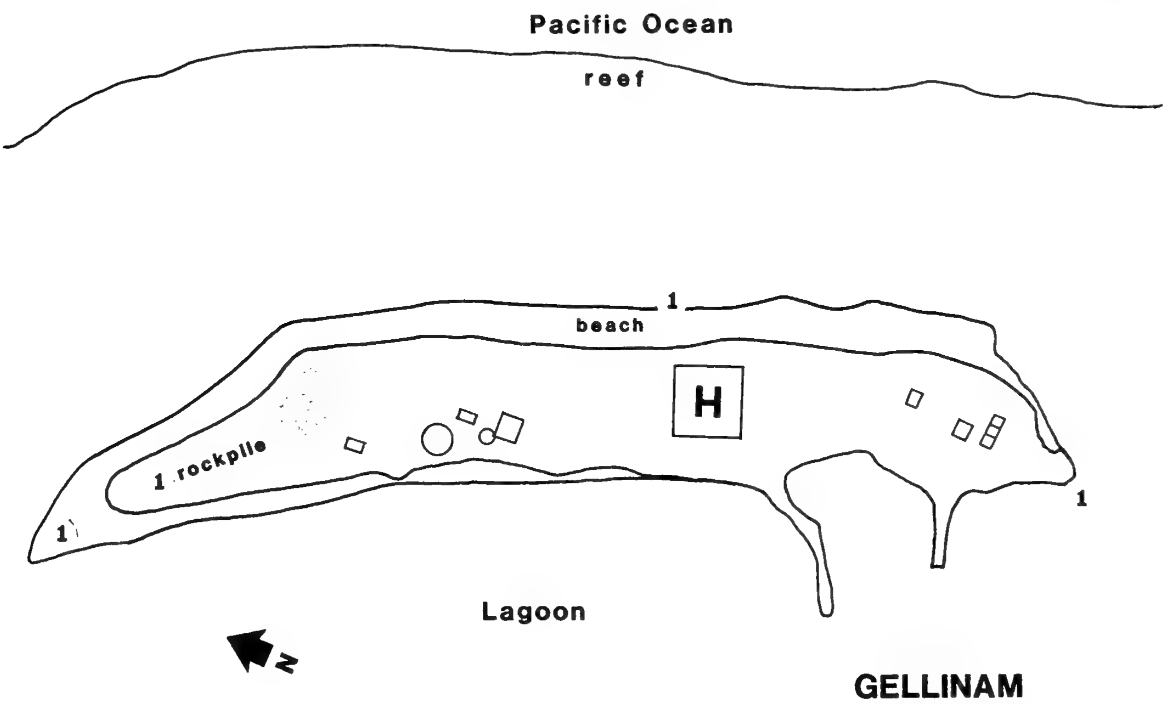

Figure 18. Gellinam Island. (1) Roosting area of Black-naped Terns. Shaded portion shows area occupied by nesting Black Noddies.

Figure 19. Looking southeast from northwest end of Gellinam Island. Coral rubble used for roosting by Black-naped Terns to left; Black Noddy colony in center.

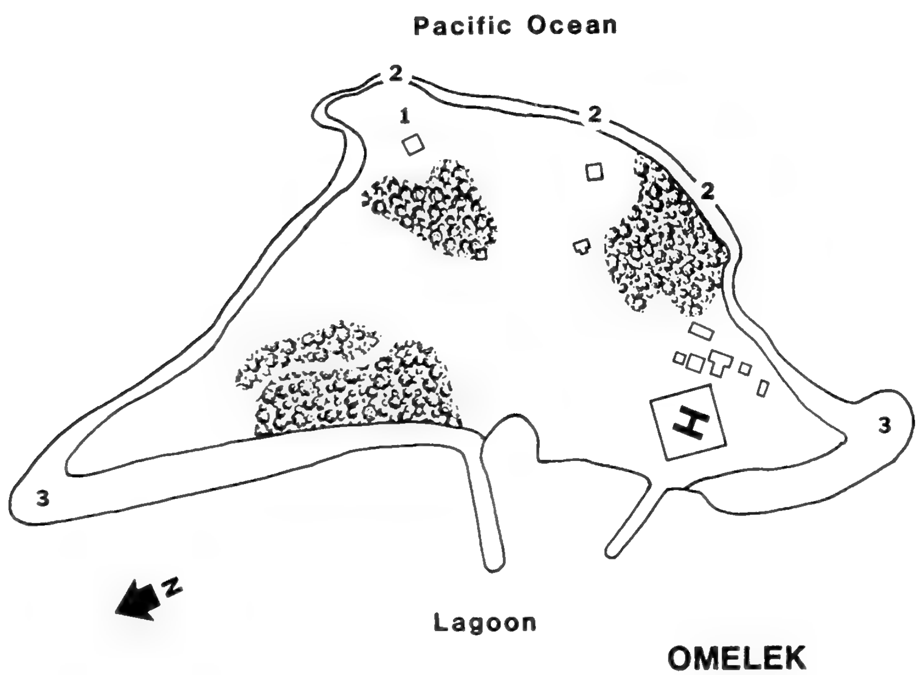

Figure 20. Omelek Island. (1) Areas where Black-naped Terns may nest; (2) other areas likely to hold Black-naped Tern nests; (3) principal roosting areas of Black-naped Terns.

helipad on the northeast point and for other facilities. The remaining area consists of scattered patches of low forest.

Eniwetak (15 acres) is within sight of Meck, is oblong, and orients west-east along the atoll rim. Two long breakwaters extend off the west end; and a helipad sits on the southeast corner (Figure 21). The southern side of the island has been cleared, and a road runs to facilities at the eastern tip. Most of the island, the northern three-quarters, holds a luxuriant Pisonia forest that is much used by nesting seabirds. That portion towards the western end of the island is more open (Figure 22); the densest, largest remaining forest, and that used to a greater degree by Black Noddies is towards the eastern end. Southern and eastern shores have emergent reef and rocky rubble. A sand beach, the widest seen on the survey, extends from the northeast along the north side of the island to the southwest.

Meck has 55 acres that extend almost north and south. More developed than the other islands surveyed, it was enlarged from fill and retains few natural features. The eastern half and southeastern two-thirds of the island are occupied by an airstrip that has a helipad about two-thirds of the way towards its northern tip (Figure 23). The portion of the island east of the airstrip is largely occupied by buildings and warehouses. The northeastern portion is elevated perhaps 40 feet or more (Figure 24) and contains various facilties. Most of the island is bordered by rough stone walls. The only sandy beach is found along the northwestern perimeter.

Kwajalein is the largest island of the group (748 acres), and it forms a crescent at the southeastern corner of the atoll (Figure 25). The island is highly developed and virtually no natural habitat is left. Most of the northeastern portion of the island is residential with large numbers of imported plants. Along the northern shore are piers, docks, a dump, and a wide variety of shops, warehouses, and other facilities. The southern portion of the crescent is largely taken up by aircraft facilities and the runway. Northwest of the runway is "Mount Olympus," a man-made area 70 feet high and the first site of missile launches from the atoll. A golf course and a fenced enclosure containing ammunition bunkers fill the area between the runway and the beach. Southeast of Mount Olympus and beyond the southwest end of the runway is an elevated area that overlooks much of the southeastern portion of the island. This elevated area ("the Plateau") and areas south and west of the runway provide the best habitat for migratory shorebirds on the island (Figure 26). These areas receive little disturbance during the week but the activities of cyclists and joggers on the weekends keep the birds somewhat wary.

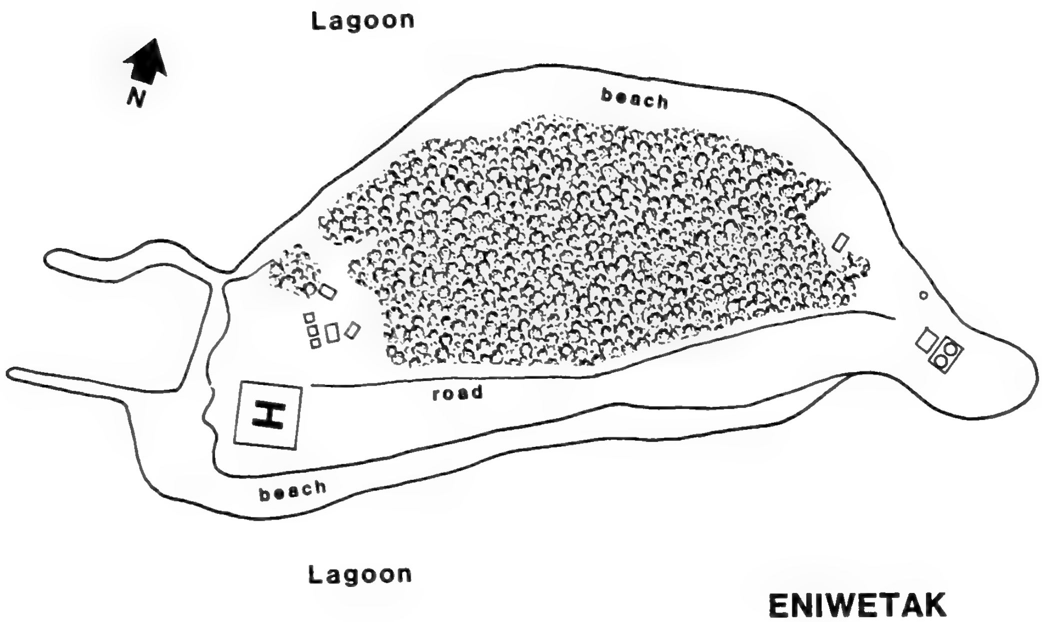

Figure 21. Eniwetak Island. Black Noddies nest throughout the forested area but are more abundant in the northern and eastern portions.

Figure 22. More open forest along north shore of Enewetak Island, looking east.

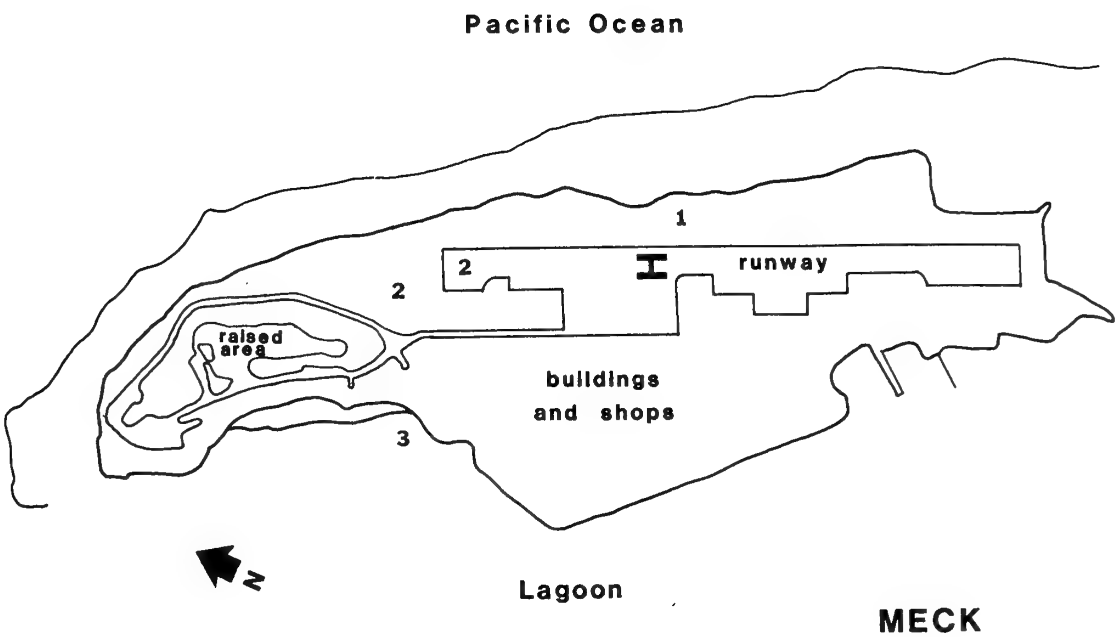

Figure 23. Meck Island. (1) Nesting area of Black-naped Terns; (2) primary shorebird roosting areas; (3) area preferred for foraging by Crested Terns.

Figure 24. Looking towards raised northwestern portion of Meck Island. Area in foreground is preferred roosting area of shorebirds.

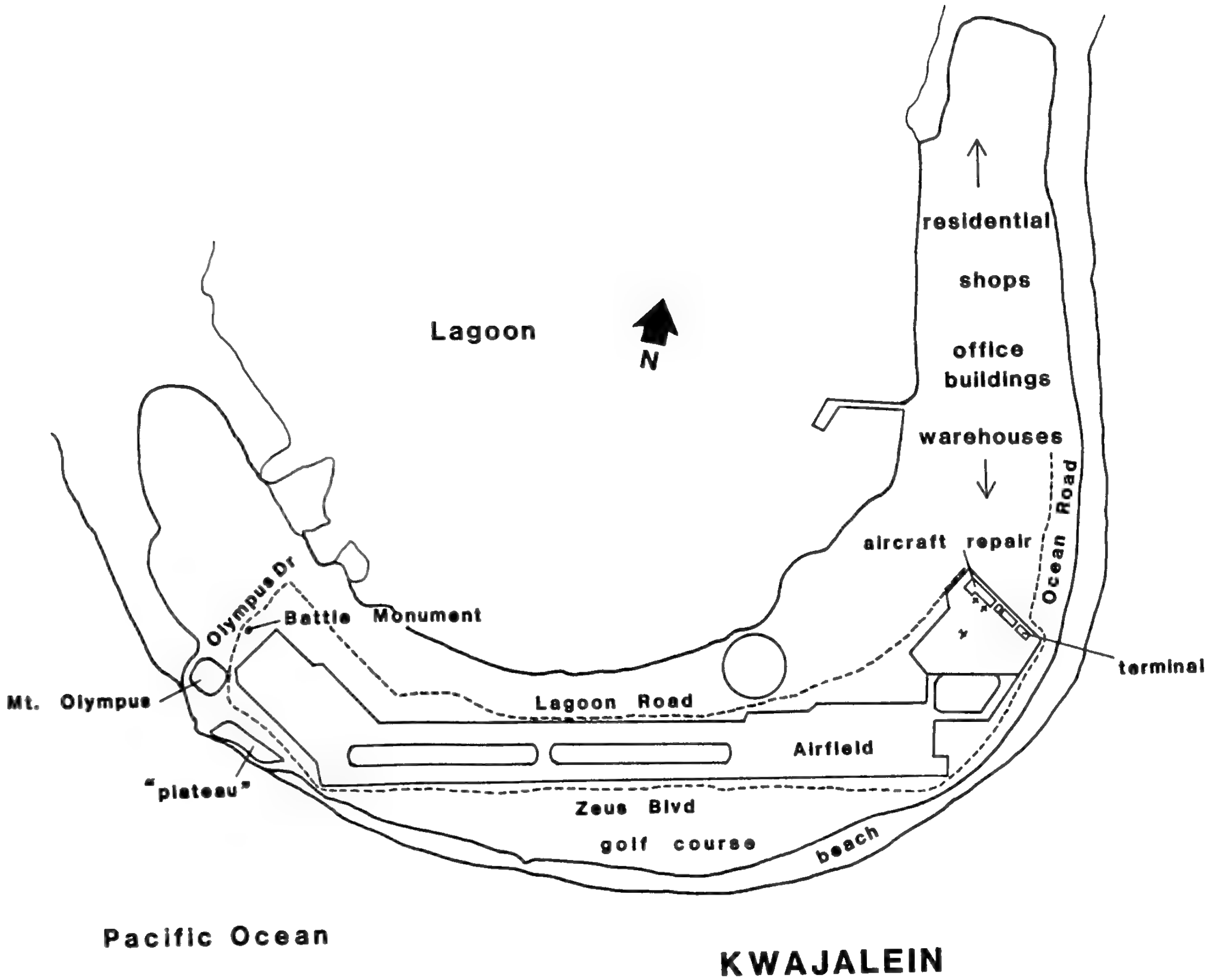

Figure 25. Kwajalein Island. Dotted line shows route of shorebird surveys.

The Avifauna of Kwajalein Atoll

The principal ornithological summaries of the Marshall Islands are Baker's (1951) "Avifauna of Micronesia" and Amerson's (1969) "Ornithology of the Gilbert and Marshall Islands." The latter includes much of the information obtained by the Smithsonian Institution's Pacific Ocean Biological Survey Program (POBSP) during the mid and late 1960's. Amerson's work compiled avifaunal lists for all the atolls in the Marshall Islands and summarized the status of the birds of the area. He reported 30 species from Kwajalein.

Figure 26. Looking northwest from the elevated area on western Kwajalein towards the overrun at the west end of the runway. Lawn areas in the mid-ground were much used for foraging by shorebirds including Bar-tailed and Hudsonian Godwits and Curlew Sandpiper.

The principal source of new information for the atoll since that report is a note by Schipper (1985) that added another 16 species. This report adds eight more and deletes one to bring the total known from the island to 53. The status of these birds is briefly summarized in Table 2.

Prior to the present survey, the birds of Kwajalein and Roi-Namur were best known because they are easy to reach and because more humans live on them. Little or no information is available for the eight outer islands surveyed or on the rest of the more than 80 islets.

Recent unpublished notes and photographs of the atoll's birds, largely for Roi-Namur Island, were provided by William Schipper who keeps a daily list of the numbers of birds seen there. These lists have been helpful in determining seasonal occurrence for species such as the Great Frigatebird (Fregata minor) and provided much information on numbers and dates of occurrence that was not provided in his earlier paper. Also incorporated in this account are additional data provided by Schipper for the period April-November 1988. The number of days per month per year in which Schipper made observations is given in Appendix Table 2.

Table 2. List of the Birds of Kwajalein Atoll

Species	Status
Mottled Petrel	Rare offshore migrant.
Wedge-tailed Shearwater	Uncommon offshore visitor.
Sooty Shearwater	Common offshore migrant.
White-tailed Tropicbird	Rare visitor.
Red-tailed Tropicbird	Rare visitor.
Brown Booby	Uncommon resident. Known to breed only on Oniotto Island.
Red-footed Booby	Uncommon resident and common offshore visitor. Known to breed only on Oniotto Island.
Great Frigatebird	Uncommon resident but frequent visitor in small numbers. Known to breed only on Oniotto Island.
Pacific Reef Heron	Common resident. Known to breed only on Roi-Namur, but almost certainly breeds on other islands in the atoll.
Cattle Egret	Rare vagrant.
Canada Goose	Accidental vagrant.
Green-winged Teal	Uncommon migrant.
Mallard	Rare migrant.
Northern Pintail	Uncommon migrant.
Garganey	Accidental vagrant.
[Gadwall]	Hypothetical.
Northern Shoveler	Uncommon migrant.
Tufted Duck Accidental vagrant.	
Black-bellied Plover	Uncommon migrant.
Lesser Golden-Plover	Abundant migrant.

Table 2 (cont'd). List of the Birds of Kwajalein Atoll

Species	Status
Mongolian Plover	Uncommon migrant.
Common Ringed or Semipalmated Plover*	Accidental migrant. Not previously reported from Kwajalein Atoll.
Greater Yellowlegs	Accidental migrant.
Lesser Yellowlegs	Accidental migrant.
Marsh Sandpiper	Accidental migrant.
Wood Sandpiper	Accidental migrant.
Wandering Tattler	Common migrant.
Gray-tailed Tattler	Uncommon migrant.
Whimbrel	Common migrant.
B-istle-thighed Curlew	Uncommon migrant.
Black-tailed Godwit	Rare migrant.
Hudsonian Godwit	Accidental migrant.
Bar-tailed Godwit	Uncommon migrant.
Ruddy Turnstone	Abundant migrant.
Sanderling	Uncommon migrant.
Pectoral Sandpiper	Accidental migrant.
Sharp-tailed Sandpiper	Uncommon migrant.
Curlew Sandpiper	Accidental migrant.
Ruff	Accidental migrant.
Latham's Snipe	Accidental migrant.
Oriental Pratincole	Accidental vagrant.
Franklin's Gull	Accidental vagrant.
Great Crested Tern	Common resident. Has not been found nesting on Kwajalein but probably breeds there.

Table 2 (cont'd). List of the Birds of Kwajalein Atoll

Species	Status
Black-naped Tern	Common resident. Known to breed only on Gagan, Meck and, Gellinam; probably breeds elsewhere as well.
Little Tern	Accidental visitor.
Sooty Tern	Uncommon offshore visitor.
Brown Noddy	Common resident. Known to breed or has bred on Debuu, Edgigen, Edjell, Gagan, Illeginni, Legan and Obella Islands; probably breeds on other islands as well.
Black Noddy	Abundant resident. Known to breed or has bred on Debuu, Edgigen, Edjell, Gagan, Gellinam, Illeginni, Legan, and Obella Islands.
White Tern	Common resident. Known to breed or has bred on Debuu, Edgigen, Edjell, Eniwetak, Ennumennet, Gagan, Kwajalein, Legan, Obella, and Roi-Namur Islands; probably breeds on other islands as well.
Fork-tailed Swift	Accidental vagrant.
Sacred Kingfisher	Accidental vagrant.
Common Mynah	Introduced; now extirpated.
House Sparrow	Introduced; now extirpated.
Eurasian Tree Sparrow	Introduced; common resident.

Annotated List

English and scientific names in the species accounts and taxonomic sequence in which the species are listed follow the A.O.U. Check-list (A.O.U. 1983) for all species listed therein. English and scientific names for the rest follow Edwards (1982). The species accounts primarily provide information on numbers, habitat utilization, and breeding status. Numbers estimated for all species during this survey are also provided in Appendix Table 1. Such estimates are limited because they derive solely from diurnal observations. My

previous experience in other Pacific seabird colonies has shown that populations roosting at night might be much greater than those seen by day. In one instance, on Birnie Island in the Phoenix Group, a nocturnally roosting population of several hundred Black Noddies would have been missed completely by a diurnal survey.

During daylight, time of day continues to strongly influence population estimates. The number of birds present during the early morning and late afternoon is almost always greater than at midday when many birds are foraging at sea. This phenomenon was particularly striking in the White Terns (Gygis alba) observed at Legan. Two to three times as many birds were seen in the early morning than later in the day. Similar daily variation in numbers present has been noted in a wide variety of central Pacific seabirds, among them Red-footed Boobies (Sula sula) and Great Frigatebirds roosting on Johnston Atoll (Schreiber and Schreiber 1986).

The stage of the breeding cycle is also critical in determining population numbers. Even in equatorial Pacific seabird populations where some individuals may breed in every month, adults and young usually disperse after the young fledge. Because little information is available on breeding seasonality at Kwajalein or at other atolls in the Marshalls, I cannot be certain whether breeding species were at peak numbers during the March 1988 survey. Black Noddies, which were at roughly comparable stages of breeding on the different islets, may have been near peak numbers. Shorebirds such as the Lesser Golden-Plover (Pluvialis dominica) may use Kwajalein both as a stopping place and a wintering area. Such species are more numerous in fall when their ranks are swelled by young than in the spring when numbers are diminuished by winter attrition.

Other examples of how numbers may be estimated erroneously are discussed by Schreiber and Schreiber (1986). In one particularly vivid example, banding studies of White Terns showed that estimates of nests present might underestimate total numbers on one atoll by two orders of magnitude and that the maximum number seen at any time represented no more than 5% of the numbers using the atoll throughout the year. Thus, the estimate of 75 White Terns present on Legan in March 1988 might indicate that as many as 1,500 terns use the islet annually.

Other problems in estimating tropical seabird populations are also provided in more detail by the Schreibers. Dunnet (1980, 1982) discussed estimation problems for seabirds of colder waters. Many of the problems, such as accuracy of single surveys, are common to both areas; and the differences are more of degree than type.

For the reasons discussed in these sources, it would be best to assume that data on numbers presented herein consistently underestimate the use of Kwajalein by seabirds.

Species Accounts

MOTTLED PETREL (*Pterodroma inexpectata*)

Schipper saw a Mottled Petrel approximately 100 ft from the reef's edge at the southeastern corner of Roi-Namur on 11 June 1987 (Clapp and Schipper 1990). This sighting is the only record for Kwajalein and for Micronesia, but the species probably occurs more frequently in the tropical western Pacific than this single record might suggest.

Mottled Petrels regularly migrate through the tropical Pacific to winter in the north Pacific (A.O.U. 1983). The northward migration, primarily from mid March to May (King 1970, Nakamura and Tanaka 1977, Ainley and Manolis 1979), largely passes through the western Pacific with smaller numbers passing through Hawaii. Presumably the bird off Roi-Namur was a late migrant.

WEDGE-TAILED SHEARWATER (*Puffinus pacificus*)

Wedge-tailed Shearwaters are uncommon offshore visitors to Kwajalein that were first reported by Anderson (1981) who saw three or four off the eastern side of the atoll on 3 July 1976. Schipper (1985) subsequently recorded them off Boggerik Island on 10 May 1980 and off Roi-Namur 24-30 May 1981. In 1987, they were recorded from Roi-Namur on seven occasions from 13 May to 15 July with a peak of 13 birds on 21 June, but they were recorded only once in 1988 when three were seen on 9 July (Schipper in litt.)

This species breeds widely on islands of the tropical Pacific (A.O.U. 1983), but in the Marshall Islands it has been found breeding only on Taongi, Bikar, Taka (Amerson 1969), and Enewetak Atolls (Hailman 1979, Temme 1990).

SOOTY SHEARWATER (*Puffinus griseus*)

Sooty Shearwaters are common off Kwajalein during migration but were not recorded there until 20 November 1979 when Schipper (1985) found a carcass along a road on Roi-Namur (Figure 27). Schipper (in litt.) has seen migrants offshore from mid May (13 May 1987, 16 May 1983) to early July (5 July 1987) with an isolated sighting on 7 August 1982. A dying bird found 25 May 1981 and sightings of about 200 passing offshore on 22 and 23 May 1981 (Schipper 1985) and of 5 and 10 birds, 13 and 14 June 1987, respectively, suggest a peak migration in late May and early June.

These shearwaters are common migrants in the central Pacific and have been recorded at sea in the Marshalls as early as April (1967) (Amerson 1969). The only previous reports from the Marshalls are one of two birds seen near Majuro Atoll on 10 or 11 June 1966 (Amerson

Figure 27. Sooty Shearwater found dead at Roi-Namur 20 November 1979. Photograph by W. L. Schipper.

1969) and two seen at Bikini Atoll 16 May 1986 (Garrett and Schreiber 1988).

Amerson reported this species and the Short-tailed (Slender-billed) Shearwater (Puffinus tenuirostris) from Eniwetak Atoll citing Pearson and Knudsen (1967). These authors only stated that either or both species had been sighted and did not specifically confirm the presence of either. The only unequivocal record for the Marshall Islands is an adult female collected at Kinajon Island on 21 April 1933 (Yamashina 1940). This record, mentioned by Baker (1951) and Serventy (1953), was later reported as a record from Ine Island, Arno Atoll by Amerson (1969).

WHITE-TAILED TROPICBIRD (Phaethon lepturus)

The only record for Kwajalein Atoll is an adult that Schipper (1985) saw flying over Ennubirr Island on 25 May 1981. This pantropical species is widespread in the Pacific but is a relatively uncommon breeder in the Marshall Islands, where it has been found breeding only on Bikar, Erikub, and Jaluit Atolls (Amerson 1969).

Amerson also listed this species as a breeding bird of Enewetak Atoll based on Woodbury's (1962) comment that "A single bird flushed

from scaevola shrubs where it was obviously nesting but the nest was not found, March 17 [1962], Kate [Muzin] islet. This was the only bird observed but it was near red-tailed [tropicbird] nests." This statement does not adequately document breeding because the habitat and situation in which the bird was found are atypical for the species. Very likely that the bird was simply resting in the area.

RED-TAILED TROPICBIRD (Phaethon rubricauda)

An adult seen flying over Omelek Island at 0929 on 17 March 1988 is the only record for Kwajalein Atoll (Clapp and Schipper 1990). The bird lacked the central tail feathers and the bill was salmon rather than the bright reddish-orange usually found in central Pacific representatives of this bird. The Red-tailed Tropicbird breeds widely in the tropical Pacific and in the Marshalls has been found nesting at Taongi, Bikar, Taka, and Enewetak atolls (Woodbury 1962, Fosberg 1966, Pearson and Knudsen 1967, Carpenter et al. 1968, Amerson 1969).

BROWN BOOBY (Sula leucogaster)

Brown Boobies breed widely in the Marshall Islands (Amerson 1969) but are uncommon on Kwajalein where they are only known to breed at Oniotto Island (Schipper 1985). The size of the breeding population is unknown, but it is probably quite small judged by how seldom birds are seen elsewhere on the atoll. None were seen during the March 1988 survey.

Brown Boobies are seen regularly off Roi-Namur where Schipper's observations (1985, in litt.; Table 3) indicate that they occur more frequently from May to November. Peak numbers seen were 10 or more on only 6 days: 20 on 10 February 1985, 15 on 26 September 1987, 11 on 11 April 1983, and 10 each on 2 August 1981, 10 June 1987, and 27 September 1987.

Fosberg (field notes) recorded a Brown Booby flying with frigatebirds at Eniwetak Island on 23 January 1952, and others were seen on buoys and feeding offshore the atoll in the mid 1960's (Amerson 1969).

RED-FOOTED BOOBY (Sula sula)

A Red-footed Booby flying off the northern side of Roi-Namur on 26 March was the only one I saw during the survey. This species has been found breeding on Kwajalein Atoll only on Oniotto Island (Schipper 1985), but it is a common breeder elsewhere in the Marshalls (Amerson 1969). No information is available on the size of the breeding population or on breeding habits at Kwajalein.

Table 3. Numbers and frequency of occurrence of Brown Boobies seen by at Roi-Namur, October 1979-November 1988 (1).

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
2)	1.3	20.0	1.8	6.0	3.2	2.5	1.9	6.7	6.3	5.0	2.2	0.0
3)	3	1	6	2	12	8	8	3	7	7	10	0
4)	.09	.03	.09	.04	.18	.13	.11	.06	.13	.10	.16	.00

1) Number of days per month and per year in which Schipper tabulated observations is given in Appendix Table 2.
2) Mean number seen for days in which observed.
3) Numbers of days observed during month.
4) Percentage of days in month of observation in which seen.

Red-footed Boobies have been seen with great regularity off Roi-Namur Island (Schipper in litt.), occasionally in large numbers. Such flocks are probably birds foraging from colonies on nearby atolls.

Analysis of Schipper's observations reveals no particular seasonal pattern of occurrence or abundance. He has recorded flocks of more than 125 birds on five occasions: 400 on 25 May 1987, 310 on 10 October 1980, 189 on 31 March 1983, 148 on 25 July 1980, and 128 on 13 July 1980.

GREAT FRIGATEBIRD (*Fregata minor*)

This species was seen only occasionally in March 1988. Two roosted atop a tall *Pisonia* tree on Eniwetak Island on 18 March, and a dead one was found along the shore at the beach crest. Another was seen flying over the north point of Ennylabagen on 23 March, and one flew over the northeastern residential portion of Kwajalein Island on 24 March. Two flew over the west-central portion of Legan the same day, and two more flew over the north portion of Namur on 26 March. These birds have also been recorded at Loi Island (Baker 1951) and an unknown number breed on Oniotto Island (Schipper 1985).

All birds seen during the March survey were adult females. Schipper (1985) has also observed a preponderance of females at Roi-Namur and other islands in the northern portion of the atoll.

Observations of frigatebirds at Roi-Namur suggest more frequent occurrence there December-July (Table 4) with peaks occurring during periods when few of the species breed at other central Pacific breeding stations. Because this species migrates west from central Pacific breeding stations following breeding (Clapp unpub.), it seems

Table 4. Numbers and frequency of occurrence of Great Frigatebirds seen by Schipper at Roi-Namur, October 1979-November 1988.

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
1)	1.0	4.0	1.8	1.7	2.7	1.6	1.5	2.0	0.0	1.5	1.0	1.0
2)	6	8	22	15	17	12	8	3	0	4	3	3
3)	.17	.21	.32	.31	.26	.20	.11	.06	.00	.06	.05	.14

1) Mean number seen for days in which observed.
2) Number of days observed during month.
3) Percentage of days of observation in which seen.

likely that a fair proportion of the birds seen at Kwajalein are transients.

Numbers seen at Roi-Namur, or at other islets of the atoll, are usually four or less on any given day. Peak numbers seen on Kwajalein Atoll are: 30 during a flyover of Oniotto on 10 February 1980 (Schipper 1985, in litt.), many dozens over Kwajalein Island on 23 January 1952 (Fosberg 1966), and nine and seven over Roi-Namur on 16 May 1982 and 9 March 1980, respectively.

PACIFIC REEF HERON (Egretta sacra)

Reef Herons occur widely on Kwajalein (Schipper 1985) and have been reported previously from Ebeye, Enebuoj, Enelakken, Kwajalein, Loi, Lojjaiong, Lojjairek, and Roi-Namur islands (Yocum 1964, Fosberg 1966, Amerson 1969, Schipper 1985).

Sightings of birds on islands visited more than once and observations at Roi-Namur (Schipper 1985) suggest that Reef Herons tend to remain in the same locality. The total using the atoll is unknown, but it the entire population on the atoll is probably no more than 100 birds.

Breeding at Kwajalein Atoll was first documented in April 1987 when Schipper (pers. comm) found a pair nesting about 8-10 ft up a Pandanus tree. The nest (Figure 28) was found when Schipper noticed a white morph bird repeatedly flying in a line towards the heavily vegetated "jungle" portion of northern Namur. This bird had breeding plumes and often displayed them when alighting at the nest. A single downy chick was first noted 25 May and at least two downy young were present by 29 May. When the young fledged is unknown, but they were still in the nest on 26 June. One of these young, identified by its distinctive mottled plumage, was sitting on the edge of a rectangular cement pond on 7 September 1987 and was seen on Roi-Namur again in the spring of 1988.

Figure 28. Nest site of Reef Heron in Pandanus on Roi-Namur. Photograph by W. L. Schipper, September 1979.

Reef Herons probably breed at other islands of Kwajalein Atoll, but no nests were found in March 1988 despite careful searches of potential nesting areas. Records of breeding elsewhere in the Marshalls (Anderson 1981, Carpenter et al. 1968) and in the western Pacific (authors cited in Baker 1951) suggest peak breeding in June and July; but egg sets taken in Polynesia (Mayr and Amadon 1941) suggest a more extended breeding season in other parts of the range.

Birds seen during this survey mostly foraged in tide-pools and on reef-flats (Figure 29), where they presumably took fish, crustaceans, and mollusks (cf. Marshall 1951, Woodbury 1962). Others foraged on grassy areas, but usually near the shoreline. Birds on Ennylabagen seemed particularly prone to feed in grassy fields; they also feed in such areas on Roi-Namur (Schipper pers. comm.). Food taken in grassy areas is presumably largely insects and other invertebrates, but Schipper (pers. comm.) has noted them feeding on lizards and rats. They have previously been recorded capturing the Azure-tailed Skink (Emoia cyanura) at Arno Atoll in the Marshalls (Marshall 1951) and presumably do so at Kwajalein. Local informants also said that they feed on rats on Ujai Atoll (Fosberg, pers. comm.)

Reef Herons occur in three plumage morphs: completely white; dark blue-gray: and "mottled," white variegated with varying amounts of blue-gray. The latter are not juveniles as birds are known to breed

Figure 29. "Mottled" Reef Heron foraging in tidal pool along the northwestern shore of Roi Island, 26 March 1988.

in these plumages. Mayr and Amadon (1941) indicated that both gray gray and mottled birds also had gray and mottled juvenal plumages, but they also pointed out that the juvenal plumage of the white morph is mottled. Consequently, the proportion of mottled birds in the population should be greatest following the breeding season and remain high until juveniles molt into the first adult plumage.

Observations during this survey, compared with those made at Eniwetak Atoll (Table 5), seem fairly consistent with a summer breeding peak although the ratios reported by Temme (in Hailman 1979) seem anomalous. Mayr and Amadon's ratio of color morphs for Micronesia was based on museum specimens and varies drastically from other observations reported from the Marshalls. It may have resulted from a selective bias if collectors avoided taking mottled birds on the assumption that most were juveniles.

Numbers of birds seen and the number of each plumage morph observed are summarized by island below.

Ennylabagen - Two were seen 9 March, four 10 March, and not less than five on 22 March. The birds (two blue, two mottled, one white) were seen along the perimeter and in the fields northwest and

Table 5. Proportions of Reef Heron color morphs observed at Kwajalein Atoll and elsewhere in the Marshall Islands (1)

Area or Atoll	Total Birds	Period	Percentage of birds white	mottled	gray	Sources
Micronesia	50	Throughout year	40	6	54	(2)
Ujelang	45	Throughout year	29	31	40	(3)
Eniwetak	57	Jun.-Sep. 1966	47	25	26	(4)
Eniwetak	13	Nov. 1977	31	31	38	(5)
Eniwetak	23	Mar.-Apr. 1978	26	26	48	(6)
Bikini	19	May 1986	58	11	32	(7)
Kwajalein	26	Mar. 1988	31	42	27	(8)

(1) Table adapted from Hailman (1979); (2) Mayr and Amadon 1941; (3) Anderson 1981; (4) Carpenter et al. 1968; (5) Hailman 1979; (6) Temme _in_ Hailman 1979; (7) Garrett and Schreiber 1988; (8) this study.

northeast of the helipad. The birds seemed to prefer the northwest shore where as many as four were seen at once.

Legan - Two were seen 11 March, a white bird foraging at the north end of the interior lake and a dark morph that flushed from the rough coral shore along the southwestern portion of the island. Four were present 24 March, a mottled bird that flushed from the north end of the lake to alight 20 feet up a palm, two white birds that flew over the interior lake, and a dark bird that flushed from the northern shore.

Illeginni - Six Reef Herons were present on 14 March and at least five were present 22 March. The plumage ratio of 14 March (two blue: three mottled: one white) varies from that seen 22 March by only the increase of one mottled bird. Birds were most abundant from the northwestern coast to the northeastern shore and at low tide foraged in pools just north of the main part of Illeginni and around the isolated sandy island just to the north.

Roi-Namur - During my visits to Roi-Namur, herons were most frequently seen along the southwestern shore of Roi and in tide-pools off the northern end of the runway. A minimum of four were present 26-27 March, one white, two mottled, and one blue-gray.

Gagan - One strongly mottled bird foraged from the northern two-thirds of the western beach to the northern point on 15 March. A white bird foraged in tide-pools along the western side on 25 March and rested there on a large concrete block.

Gellinam - None seen.

Omelek - One white bird foraged on the western reef at low tide on 17 March.

Eniwetak - None seen.

Meck - None seen.

Kwajalein - A strongly mottled Reef Heron foraged in a tide-pool among grass east of Mt. Olympus on 12 March, and a lightly mottled bird fed there on 17 March. A bird with entirely white plumage flew over the outer reef south of the runway on 19 March, and a white bird with a blue patch on the back foraged around a raised bunker near there on 20 March.

The absence of Reef Herons from the residential and work areas of the island presumably results from continual disturbance by the inhabitants. More probably occur at Kwajalein Island than I recorded, but the numbers there are proportionately lower than at some of the less disturbed islands with much smaller reef areas.

CATTLE EGRET (*Bubulcus ibis*)

This rare visitor to Kwajalein was first seen there when a bird in breeding plumage was found on the southern end of Roi-Namur on April 1980. It was last seen on 10 May, but another was seen near the Caribou Lounge on Kwajalein Island on 24 October 1981 (Schipper 1985). Schipper (1985) suggested that this was the same bird seen nearly 17 months earlier, but I think it more likely that it was a different individual. Schipper (in litt.) saw another Cattle Egret at a rain pool on Roi-Namur on 1 March 1987. This bird was seen on eleven other occasions during the ensuing two months and was last seen on 28 May.

Cattle Egrets are widespread and common migrant in Micronesia (Pratt et al. 1987) and are also an abundant introduced resident in the main Hawaiian Islands. The birds seen on Kwajalein could have been from either the western Pacific or Hawaii.

CANADA GOOSE (*Branta canadensis*)

Two banded Aleutian Canada Geese (*B. c. leucopareia*) that straggled to Roi-Namur in late 1979 (Schipper 1985, Springer et al. 1986) are the only ones recorded in the Marshall Islands. The first goose was seen about 26 November and died a few days later; the second was observed 3-6 December. Both birds were from a deme listed as an "endangered species" by the U. S. Fish and Wildlife Service. They had been reared at Amchitka Island in the Aleutian Islands National Wildlife Refuge and were transplanted with other birds 250 miles west to Agattu Island in the western Aleutians. The geese had

been taken there in the hope that the young would follow wild adults to the usual wintering grounds in the San Joaquin Valley of California. Two of these geese instead wandered some 3,000 miles south to Kwajalein Atoll.

This species occurs regularly in Hawaii but is rarely found in more tropical waters. Pratt et al. (1987) indicated, without reference, a record of one or more birds at Tarawa in the Gilbert Islands (now Kiribati). If valid, this record would be the only other Pacific record south of Hawaii. Aside from an introduced population in New Zealand (A.O.U. 1983), the records of Canada Geese from Kwajalein (at ca $9^{0}20'$ N) and Tarawa (ca. $01^{0}30'$ N) are the southernmost known occurrences for the species.

GREEN-WINGED TEAL (Anas crecca)

These teal, uncommon migrants to the Marshall Islands, have been recorded four times at Kwajalein Atoll. According to a secondhand account (Yocum 1964), a flock of about 74 was present on Kwajalein sometime between September 1959 and February 1960. The other records are for three female-plumaged ducks seen on Roi-Namur, one in November 1978, another in 31 October 1979, and a third on 1 January 1980 (Schipper 1985).

Green-winged Teal occur regularly in the Hawaiian and Marianas Islands (Pratt et al. 1987), but there are very few records for more tropical islands. South of these northern groups, this teal has been recorded on Angaur Island, Palau (Engbring and Owen 1981), on Jaluit in the Marshall Islands (Reichenow 1901, Schnee 1901), and on Palmyra Atoll in the Line Islands (Clapp and Sibley 1967).

MALLARD (Anas platyrhynchos)

The only published record of Mallards on Kwajalein (and in the Marshall Islands) is a secondhand report of two flocks of about 12 birds each that were seen on Kwajalein Island during the winter of 1959-60 (Yocum 1964). Ducks were seen at Illeginni Island on three occasions during the past several years; at least one was a drake Mallard (K. Jourdan, pers. comm.)

Mallards are relatively uncommon migrants to the tropical Pacific and have been seen most frequently, if irregularly, in the main and northwestern Hawaiian Islands. Elsewhere in the tropical Pacific, the species has been recorded at Tarawa in the Gilbert Islands (Child 1960), at Sarigan in the northern Mariana Islands, on Yap (Pratt et al. 1987), on Palmyra in the Line Islands (Munro 1944), and on Penrhyn, Suvarov, and Pukapuka Islands in the northern Cook Islands (Pratt et al. 1987).

NORTHERN PINTAIL (Anas acuta)

Northern Pintails are the most widespread and abundant of anatid migrants to the tropical Pacific. They have occurred more frequently on Kwajalein Atoll than any other duck, with all dated records occurring from November to March.

"Several" were seen on Kwajalein Island during the winter of 1959-60 (Yocum 1964) and six specimens, two males and four females, were collected from rain pools along the runway on 2 to 9 November 1964 (Amerson 1969). Schipper (1985, in litt.) has since recorded female-plumaged birds frequently during the fall and winter on Roi-Namur and on Kwajalein. One or more were seen on Kwajalein and Roi-Namur in November 1978 (Schipper 1985), and one or more were seen on Roi-Namur in March 1979. Subsequent observations on Roi-Namur are of one to three ducks seen on 18 October-23 November 1980, one to two seen on 23-27 October 1981, a flock of 12 on 5 November 1987 of which one to two were present to 19 November with one remaining until 21 December, and two to seven seen repeatedly during the period 27 September-11 November 1988. Eight, five, and 14 were seen on Kwajalein on 8 and 12 October and on 5 November 1988, respectively.

[GARGANEY (Anas querquedula)]

Schipper saw a male in winter plumage on Roi-Namur on 2 November 1988 (Figure 30) as it foraged with several Northern Pintails (Clapp and Schipper 1990). This Paleartic breeder winters south to eastern China, New Guinea, and Australia (A.O.U. 1983) but has been recorded infrequently in the tropical Pacific except for the Mariana Islands where it regularly occurs (Glass et al. 1990).

Elsewhere, the species has been recorded in Palau (Pratt et al. 1987) and has been seen more than a dozen times in Hawaii (Spear et al. 1988). The only other record from the tropical Pacific is from Wake Island where two specimens were collected 23 December 1983 (Clapp and Schipper 1990).

NORTHERN SHOVELER (Anas clypeata)

This widespread holarctic duck has been recorded on Kwajalein five times. An unspecified number, one of which was shot, were present on Kwajalein Island in the fall and winter of 1959-60 (Yocum 1964); and two, a male and an unsexed bird, were collected there on 3 November 1964 at fresh water ponds along the runway. Schipper (1985, in litt.) thrice found them on Roi-Namur, one female-plumaged bird on 2 November 1980, another on 5 November 1987, and 1-3 from 7-31 October 1988.

The Northern Shoveler winters commonly in Hawaii and irregularly in small numbers in Micronesia (Pratt et al. 1987) but is much less

Figure 30. Garganey (center) with Northern Pintails on Roi-Namur Island. Photograph by W. L. Schipper, 2 November 1988.

common elsewhere in the tropical Pacific. Other atolls at which it has been recorded include Makin (North 1894) and Tarawa (Morris 1963) in the Gilbert Islands, Palmyra in the Line Islands (Clapp and Sibley 1967), and at Kauehi in the Tuamotus (Baker 1951).

GADWALL (Anas strepera)

Yocum (1964) reported that W. W. Fennell found this to be the most numerous of more than 200 ducks seen on Kwajalein during the winter of 1959-60. This implies that perhaps 100 birds were present as Fennell indicated that he had seen 75 teal in one flock.

While the other species of ducks reported by Fennell are among those fairly widespread as migrants or vagrants in the Pacific, this record of the Gadwall is the southwesternmost report of this species in the tropical Pacific and the only record west of the Hawaiian Islands. Even in Hawaii the species is uncommon and a report of that many Gadwall there would immediately rouse suspicions as to the competence of the observer. Pyle and Engbring (1985) regarded this record as probably erroneous, and it seems best to remove this species from the list of those known to occur at Kwajalein.

TUFTED DUCK (*Aythya fuligula*)

This Palearctic diving duck occurs casually in the Hawaiian Islands and in western Micronesia (A.O.U. 1983, Pratt et al. 1987). The one Kwajalein record is a female that I collected (USNM 494852) on 2 November 1964 from ponds along the edge of the runway on Kwajalein Island (Amerson 1969). The specimen is a young of the year and was very light (423 g), suggesting that it was starving.

Shorebirds

Almost 40% of the birds known from Kwajalein are sandpipers and plovers. Many are migrants but others remain to winter. These shorebirds typically comprise a third or more of all species seen on surveys of tropical islands conducted during migrations. This was also true in March 1988, with shorebirds comprising 10 of the 20 species observed. Shorebirds find the grassy fields of the golf courses on Kwajalein and Roi-Namur and other open areas of these islands, and those on Meck and Ennylabagen, good areas for foraging. Runways, taxiways, and helipads are much used as resting areas. As a consequence, shorebird populations, with the likely exception of reef-foraging tattlers, are probably larger on the environmentally more disturbed islands than when the islands were unmodified. In some instances, as on Kwajalein, Meck, and Roi-Namur, shorebirds comprise the vast majority of birds present.

During this survey, I periodically counted all the birds that could be seen on Kwajalein Island with an 8x, 30 binocular. The route went from the Sand's bachelor's quarters south along Ocean Drive and around the airstrip on Zeus Boulevard, Olympus Drive, and Lagoon Road ending at the aircraft repair shop (Figure 22). This allowed census of all shorebirds except for a very small proportion on the south side of the golf course and the magazine bunkers. Approximate times at which censuses were conducted are given in Appendix Table 3.

Similar counts were made on Roi-Namur on 12, 26, and 27 March. The latter two were on a route around the airstrip and west on Pandanus Road, south on Speedball Road, and then east at Explosive Storage Building Number 1 (building 8002 in Global Associates 1987) to the south end of the airstrip. The survey on 12 March was similar but followed Speedball Road to the south end of the airstrip. These routes provided relatively less coverage of the entire island than did the one on Kwajalein. Totals for the 12 March count were much lower than those on 26 and 27 March and only the latter were considered in making the final estimate of island populations.

I also explored other areas of Roi-Namur to determine the proportion of the shorebird populations that was represented by the area censused. Because much of Namur provides only mediocre shorebird habitat, I consider that my counts represented probably

about 85% of the Ruddy Turnstone (Arenaria interpres) population, 75% of the Lesser Golden-Plover population and perhaps no more than 60% of the Whimbrel (Numenius phaeopus) population.

Numbers of shorebirds observed during the counts on Kwajalein are summarized in Table 6. Totals for Lesser Golden-Plovers and Ruddy Turnstones were adjusted to include birds counted on the grass in front of the terminal but that usually could not be identified to species because of poor lighting and distance from the observer. Two Wandering Tattlers (Heterocelus incanus) and a Bristle-thighed Curlew (Numenius tahitiensis) were seen in the count area but not during formal counts.

Counts on other islands (Table 7) show that the Ruddy Turnstones and Golden-Plovers also are the most abundant shorebirds there. Counts of Golden-Plovers, Whimbrels, and Ruddy Turnstones at Roi-Namur (Tables 8, 9, 12) suggest that populations decline in March and increase in April before dropping to summer lows. Some of the wintering birds may depart in March before migrants arrive from the south.

Table 6. Shorebird counts[1] made on Kwajalein Island in March 1988.

Date	Time	RT	LGP	WH	HG	BTG	STS	CS
20th[2]	1800-1915	(230)	(177)	6	-	1	-	-
23rd	1653-1831	417[3]	184	5	1	-	-	1
24th	1700-1832	323	184	4	-	-	7	-
25th	1627-1808	372	151	3	1	-	6	1
28th	0713-0846	213	158	5[4]	-	1	13	-
28th	1520-1639	337	93	5	-	-	1	-
29th	0830-0957	289	149	3	1	1	4	1

(1) RT: Ruddy Turnstone, LGP: Lesser Golden-Plover, WH: Whimbrel, HG: Hudsonian Godwit, BTG: Bar-tailed Godwit, STS: Sharp-tailed Sandpiper, CS: Curlew Sandpiper
(2) Because of a rainsquall this count went only as far as the invasion battle monoment.
(3) This count is probably too high because birds seen flying into the tarmac near the aircraft shop late in the day may have been counted earlier around the airstrip.
(4) Includes three birds counted on the plateau at the northwest end of the airstrip.

Table 7. Counts and estimates of shorebird[1] numbers on the other islands in March 1988

		RT	LGP	Tat.	WH	BTC	BTG	Totals
ENN[2]	9th	65 (75)[3]	94 (125)	2 (10)	9 (10)	-	-	170 (220)
	10th	27 (40)	88 (100)	12 (20)	7 (8)	-	-	134 (168)
	23rd	49 (60)	88 (100)	4 (15)	6 (8)	-	-	147 (183)
LEG	11th	21 (25)	16 (20)	10 (10)	-	2	-	49 (77)
	24th	19 (25)	13 (15)	4 (10)	-	2	-	38 (52)
ILL	14th	11 (15)	13 (15)	7 (10)	4	1	-	36 (45)
	22nd	19 (20)	25 (30)	5 (10)	3	1	-	53 (64)
GAG	15th	2	5	1	-	-	-	8
	25th	1	3	1	1			6
GEL	9th	9	4	1	-	-	-	14
OME	17th	10	3 (5)	2	1			15 (18)
ENI	19th	-	6	1	-	-	-	7
MEC	20th	16 (20)	57 (60)	1 (3)	5 (7)	-	1	80 (91)
Totals[4]		141 (161)	210 (255)	35 (48)	20 (23)	3	1	410 (491)

(1) RT: Ruddy Turnstone, LGP: Lesser Golden Plover, Tat.: tattlers (all tattlers heard but one appeared to be Wandering Tattlers), WH: Whimbrel, BTC: Bristle-thighed Curlew, BTG - Bar-tailed Godwit
(2) ENN: Ennylabagen, LEG: Legan, ILL: Illeginni, GAG: Gagen, GEL: Gellinam, OME: Omelek, ENI: Eniwetak, MEC: Meck.
(3) Figures alone are raw counts; those in parentheses give estimates if these differ from the counts.
(4) Totals include the largest estimate and count if more than one visit was made to an island.

BLACK-BELLIED PLOVER (*Pluvialis squatarola*)

Black-bellied Plovers have been recorded at Kwajalein four times. A female was collected (USNM 494822) on Kwajalein Island on 3 November 1964 (Amerson 1969) and at least three sight records exist for Roi-Namur. Schipper (1985, in litt.) saw one there on a sandy beach on 15 November 1981, another was present 3 February to 17 August 1987 and a third was seen and photographed during the period 16 March-6 April 1988 (Schipper in litt., pers. comm., Figure 31). The second bird, in non-breeding plumage, showed no evident change in

Figure 31. Black-bellied Plover on Roi-Namur Island, March 1988. Photograph by W. L. Schipper.

plumage throughout the period. He saw a third winter-plumaged bird on Roi on 21 December 1987 at the end of the runway. It maintained a territory and vigorously chased away Lesser Golden-Plovers. A sighting on 16 March 1988 may have been of this or another bird (Schipper pers. comm., in litt.).

The only other record for the Marshall Islands is an undetailed report of seven seen on Eniwetak Atoll during late July 1945 by D. A. Gleize and D. Genelly (Anon. 1945). To this unsatisfactory record from Eniwetak may be added a specimen (USNM 544243) collected by the POBSP at Engebi Islet, Eniwetak Atoll, on 11 December 1968.

Black-bellied Plovers are uncommon winter visitors to Micronesia (Palau, Yap, Mariana Islands, Truk) and to Hawaii and have been reported once from Manuae in the Cook Islands (Holyoak 1981) and from Malden in the Line Islands (Clapp and Sibley 1967)

LESSER GOLDEN-PLOVER (*Pluvialis dominica*)

This species and the Ruddy Turnstone were found nearly everywhere on the atoll, but they differed in distribution and behavior. Plovers held territories and were relatively uniformly scattered over grassy areas. On Kwajalein Island different parts of the island held

about the same numbers of plovers from day to day (Table 8). Turnstones fed in flocks that were highly mobile and moved from one area to another.

Table 8. Numbers of Lesser Golden-Plovers and Ruddy Turnstones seen on parts of the Kwajalein Island shorebird census (1)

		Number counted on March:								
Area	Species	17	20	23	24	25	28	28	29	Mean
Golf course	GP			14	30	30	42	26	40	30.3
	RT			18	16	29	37	67	23	31.7
Runway margin	GP			49	32	22	19	13	19	25.7
	RT			45	4	15	1	20	7	15.3
Stop sign to Mt. Olympus	GP		2	14	19	14	9	4	11	10.4
	RT		19	27	42	38	16	32	16	27.1
Plateau	GP	3					1	1	1	1.5
	RT	1								.25
Battle memorial field	GP	5	12	7	3	7	8	0	12	6.8
	RT	19	12	13	23	15	1	20	7	13.8
Fields N of Mt. Olympus	GP	5	9	9	9	6	6	1	8	6.6
	RT	19	13	13	10	10	4	21	8	12.3
"Dump road" field	GP	0	6	2	3	1	4	1	3	2.5
	RT	20	4	11	10	10	1	0	5	7.6
N to Coral Sands	GP			10	14	13	16	1	9	10.5
	RT			55	60	27	13	9	8	21.5
Coral Sands to helipad	GP	15		13	14	21	15	8	18	14.9
	RT	13		5	17	35	2	15	6	13.3
"O" field	GP	2		5	-- (2)	4	4	1	5	3.5
	RT	44		48	--	50	9	8	8	27.8
Helipad field	GP			3	2	4	0	0	4	2.2
	RT			25	54	77	0	16	1	28.8
Helipad to aircraft shop	GP			5	3	4	4	0	3	3.2
	RT			1	10	27	4	0	2	7.3

(1) Times areas were surveyed and a more detailed description of the area covered are given in Appendix Table 2.
(2) No birds were present due to a softball game in progress.

Observations on Kwajalein and elsewhere in the Marshall Islands clearly show a principal period of occurrence from September through early April although a few plovers are usually present throughout the year. Judged from daily counts made on Roi-Namur (Table 9, Schipper in litt.), some spring migrants may be present into early May. Early fall migrants begin arriving on Roi-Namur in mid July (53 were counted by Schipper on 19 July 1987). Peak migration occurs in April and in September and October. Comments on plovers on individual islands are given below.

Ennylabagen - Plovers were common in the vicinity of the helipad and on nearby fields. The large field northwest of the helipad (Figure 32) held roughly 70% of the total population of about 100 birds (72, 62, and 74 counted on 9, 10, and 23 March respectively). The rest were scattered widely and rather evenly about the rest of the island. Most were in cleared areas but a few were found on trails through the forest and in ones and twos along the rocky shore.

About 5-10% of the birds seen on 9 March had attained full or nearly full breeding plumage. By 23 March perhaps 20% were in full breeding plumage.

Legan - A total of about 20 presumably represented the limited amount of habitat available in the interior of the island. About 25% were found resting or foraging on the small grassy area around the helipad with the rest found along the perimeter on both sandy and

Figure 32. Golden-Plovers (and a few Ruddy Turnstones) on Ennylabagen Island, 23 March 1988.

rubble shores. The principal concentration was on the secluded interior lake where about ten birds were found on each visit. Only a few of the plovers on the interior lake were seen foraging; the area seemed to be used primarily as a resting area.

Illeginni - Lesser Golden-Plovers on Illeginni largely occurred around the helipad, along the roads, and, at low tide, on the exposed flats north of the island. The heavy growth of Wedelia in the open areas bordering the central road denies this area to plovers or other shorebirds. The overall density of the vegetation here and elsewhere on the island would account for the low numbers (ca. 25) of plovers on an island this size. The only concentration noted was ten birds on and around the helipad on 22 March. This open area is highly attactive to this species, and the helipad itself is the primary roosting site on the island.

Roi-Namur - Counts on 26 and 27 March 1988 gave totals of 153 and 186 plovers, respectively. Assuming 80% coverage results in an estimate for the island of about 230 birds, larger than peak numbers recorded by Schipper (Table 9) for this month but representing a more thorough census. The only previous estimate of plover numbers on Roi is one of 200 birds on 4 November 1964 (Amerson 1969).

Lesser Golden-Plovers are well distributed over Roi and may be found everywhere except in heavily vegetated areas. I found no distinct concentrations but plovers as well as turnstones and Whimbrels roosted in some numbers on exposed flats on the western side of Roi.

Table 9. Numbers of Lesser Golden-Plovers seen by Schipper at Roi-Namur, October 1979-November 1988.

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
1)	56	38	47	67	14	24	17	19	53	44	41	86
2)	200	100	242	260	56	141	88	114	285	222	203	251

(1) Mean number seen per days observed. Examination of Schipper's daily tallies for shorebirds shows that these totals are often less than the number that must have been present. This is especially true for this species and the Ruddy Turnstone. Consequently, these tables provide no more than an indication of relative monthly abundance.
(2) Peak number recorded.

Gagan - On 15 March one plover was seen on the western side of the island, two on the grass around the helipad, and two more in the grass north of the helipad. Three were seen on 25 March, one on the helipad and two along the island's shores.

Gellinam - Four plovers were seen, one on the sandy southeastern beach, two near the helipad, and one with a flock of

eight Ruddy Turnstones in an open grassy area just south of the Black Noddy colony.

Omelek - One seen along the east side of the island, another in the grass at the north end, and one on the helipad.

Eniwetak - Two to three were seen in grassy areas of the island, and another four were on the rocky flats off the eastern and southeastern portion of the island.

Meck - About 50 plovers were at the northern end of the airstrip and in the low vegetation beyond. A few were seen along the shores of the island on both sandy and rocky beaches.

Kwajalein - Peak counts on 24 and 25 March were 184 birds. Two counts of the northeastern portion of the island on 19 and 20 March gave 28 and 26 plovers, respectively, and examination of areas that could not be seen on the counts suggests that other areas held about another 60 birds. I estimate a total of about 270 present in March 1988, with a small proportion in nearly full breeding plumage by the end of the month.

Plovers on Kwajalein were widely distributed (Table 8) and foraged along hard roads and in yards on the northeastern part of the island as well as in any other open area. Plovers were highly territorial, and in one instance one was seen chasing a Ruddy Turnstone. Plovers were active at night in inhabited lighted areas but were very wary. Some roosted on the roofs of buildings during the night. Roosting concentrations (to ca. 50 birds) formed on the overrun beyond the southwestern end of the runway and on the tarmac in front of the terminal.

MONGOLIAN PLOVER (Charadrius mongolus)

The records for Kwajalein Atoll are single birds seen on Roi-Namur on 10 and 12 November 1981, on 3-30 October, 6 November and 11-12 December 1982, and on 8 August 1987; three seen 3 July 1988 and two seen 21, 28 and 29 August 1988 (Schipper 1985, in litt.)

Other published records of this east Asian species in the Marshall Islands are sightings of single birds on Enewetak Islet, Enewetak Atoll in November 1977 and in the fall of 1978 (Hailman 1979), four on Aomon Islet, Enewetak Atoll on 16 November 1978 (Temme 1990), and one to two birds at Ujelang Island, Ujelang Atoll from 7 September to 5 December 1975 and from 26 November 1976 to 18 February 1977 (Anderson 1981). Hailman (1979) suggested that the records from Eniwetak might have been of the similar appearing Greater Sand Plover (Charadrius leschenaultii), but unpublished observations and collections of C. mongolus on Enewetak Atoll suggest that it is a regular visitor there (Clapp ms.).

There is but a single record for this species further east in the Pacific, one found at Lisianski Island in the Northwestern Hawaiian Islands in September 1967 (Clapp and Wirtz 1974); at least four have straggled to the western United States (A.O.U. 1983). Thus it appears that the Marshalls represent the easternmost area to which this species regularly migrates.

COMMON RINGED (Charadrius hiaticula)
or SEMIPALMATED PLOVER (C. semipalmatus)

Schipper saw one or the other of these species on Kwajalein Island on 8 and 12 October and 5 November 1988. The bird was in non-breeding plumage, in which these two are very difficult or impossible to distinguish (Pratt et al. 1987). The call note, described as a whistled "chu-weet", sounds more as if it were a Semipalmated Plover than a Ringed, but both species could occur on Kwajalein. On both days the plover was seen feeding on the northern portion of the water catchment basin between the taxiway and the runway, usually solitarily but sometimes with Ruddy Turnstones.

The Nearctic Semipalmated Plover straggles fairly regularly to Hawaii and to the eastern Pacific while the palearctic Ringed Plover has been reported on Palau, Saipan, Guam, and Midway (Pratt et al. 1987, Glass et al. 1990). Some of these records are inadequately documented, however, as is a record of the Semipalmated Plover from Jaluit.

Most of the well documented records of small Charadrius in the central Pacific are of Semipalmated Plovers. Specimens of Semipalmated Plover have been taken in Hawaii and the northwestern Hawaiian Islands (Clapp 1968a, Ely and Clapp 1973, Clapp and Wirtz 1974), on Baker Island not far to the east of the date line (Clapp 1968b), and on Johnston Atoll, southwest of Hawaii (Amerson and Shelton 1976). Thus, it seems considerably more likely that the bird (or birds) seen on Kwajalein was a Semipalmated Plover, but it is impossible to so state on the data presently available.

GREATER YELLOWLEGS (Tringa melanoleuca)

The only record for Kwajalein is a bird seen briefly at a rain-pool on Roi-Namur on 21 October 1978 (Schipper 1985). This North American breeding bird is only rarely found in the tropical Pacific. Nearly all previous records are from the main Hawaiian Islands; the only well documented record elsewhere is a male collected on Jaluit Island, Jaluit Atoll on 12 May 1932 (Kuroda 1934)

Other reports of birds, poorly documented, from Wake Island and on Rarotonga, Cook Islands (Pratt et al. 1987) as well as a recent sight record from Rota (Glass et al. 1990) may have been this species. I examined the original data for the Wake record and it is

not strong enough to identify the bird as other than either Greater or Lesser Yellowlegs, Tringa sp.

LESSER YELLOWLEGS (Tringa flavipes)

A Lesser Yellowlegs feeding with a Sharp-tailed Sandpiper at a rain-pool on Roi-Namur was seen and photographed on 27 September 1987 (Figure 33) and another foraging bird was seen on 8 November 1988 on Kwajalein Island along the northernmost catchment basin between the runway and the taxiway (Clapp and Schipper 1990).

These sightings are the only records of Lesser Yellowlegs for Kwajalein and for the Marshall Islands. This North American species is rarely seen in the tropical Pacific and along the Asiatic coast, but it has been recorded ten times in New Zealand (Clapp and Schipper 1990) and is seen regularly in Hawaii (Pratt et al. 1987). The only other records for the tropical Pacific are a specimen from Johnston Atoll (Amerson and Shelton 1976) and a recent sight record from the Tuamotu Archipelago (Intes 1988).

MARSH SANDPIPER (Tringa stagnatilis)

Late on the afternoon of 26 September 1987, Schipper saw a Marsh Sandpiper at a temporary rain pond along a dike behind water tanks on Roi-Namur. The bird was wary, but could be approached as closely as 50 feet. It was not found the following day despite a careful search (Clapp and Schipper 1990).

Figure 33. Lesser Yellowlegs foraging with Sharp-tailed Sandpiper on Roi-Namur Island, 27 September 1987. Photograph by W. L. Schipper.

This Palearctic sandpiper breeds east to Siberia (A.O.U. 1983) and winters south to Australia (Lane 1987) and is known from western Micronesia (Pratt et al. 1987). The bird on Roi-Namur is the only one recorded in eastern Micronesia or anywhere else in the central Pacific (Clapp and Schipper 1990).

WOOD SANDPIPER (Tringa glareola)

Schipper (1985) saw and photographed a single bird on Roi-Namur on 16 October 1982 following a period of steady, strong southwest winds. The only other published records for the Marshalls are of one bird seen 9 and 21 November 1977 on Aomon Islet, Enewetak Atoll, and one to three seen and photographed there 24 and 25 March and 7 and 8 April 1978 (Temme 1985). In addition, a specimen in the U.S. National Museum was collected on Enewetak Atoll on 8 September 1968 (Temme 1990).

This Paleartic species is a fairly common migrant in western Micronesia (Pratt et al. 1987, Glass et al. 1990), but has been recorded elsewhere in the tropical Pacific only in the Northwestern Hawaiian Islands (Pratt et al. 1987).

WANDERING TATTLER (Heteroscelus incanus)

Wandering Tattlers are a widespread and common migrant and winter visitor to Kwajalein Atoll with a few birds remaining during the summer. It has been previously recorded from Kwajalein, Roi-Namur, Loi, Bigej, and Guguegeegue Islands (Yocum 1964, Fosberg 1966, Amerson 1969, Schipper 1985) but always in small numbers. Said to be most common in late fall and winter (Schipper 1985), it almost certainly occurs on most islands of the atoll. Comments on birds seen at individual islands are given below.

Ennylabagen - Tattlers were scattered fairly regularly along the rocky shores of the island's western side. Probably three-quarters of approximately 20 birds found were along this shore with four together on the rocky ledges on the northwestern side of the island.

Legan - On both visits about half the population of 10 tattlers roosted or foraged in the interior lake. Most of the rest were on coral rubble lining the western shore, but one was seen on the sandy beach on the eastern side.

Illeginni - The total population of about ten seems small considering the amount of habitat available. A few were seen along the eastern and western shores but most were on flats exposed by low tide at the northern end of the island.

Roi-Namur - As on Legan, tattlers tend to concentrate on the interior lake. Fifteen were seen there at 1439 on 26 March 1988 resting on the sand beneath Pemphis bushes on the inlet's western shore (Figure 34). Others were scattered in small numbers along rocky shores at low tide, particularly on the western side of Roi and on the northeastern side of Namur. The total population of the island probably did not exceed 30 birds. I estimated that perhaps 25 birds were here on 4 November 1964 (Amerson 1969) on a less thorough survey. Schipper's observations (Table 10) at Roi-Namur suggest similar population levels and peaks, but data are too few to provide much information on periods of migration.

Table 10. Numbers of Wandering Tattlers seen by Schipper at Roi-Namur, October 1979-November 1988.

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
1)	3.4	4.0	4.1	4.0	2.0	4.5	3.6	3.4	5.3	5.9	5.9	8.1
2)	11	15	15	16	8	8	8	14	15	21	12	13

(1) Mean number seen per days observed.
(2) Peak number recorded.

Figure 34. Fifteen tattlers roosting on Roi-Namur 26 August 1982. Lesser Golden Plover walking towards camera and Pectoral Sandpiper roosting in the left foreground. Photograph by W. L. Schipper.

Gagan - The single bird seen on both visits was on flats at the northern end of the island.

Gellinam - One Wandering Tattler was seen along the eastern shore.

Omelek - Two were seen along the eastern shore on 17 March.

Eniwetak - One was present on the rocky reef-flat off the eastern and southeastern shores.

Meck - One bird was seen sitting atop large, open, coral rubble on the upper western shore. Perhaps a few more were present, but the number found is surprisingly low considering the amount of available habitat.

Kwajalein - Wandering Tattlers were seen much more frequently on the outer islands than on Kwajalein (Table 7) but this difference may result from the difference in the way these islands were surveyed. The outer perimeters of the eight outer islands were walked in their entirety while only a relatively small proportion of equivalent habitat was covered on Kwajalein.

A count I took on Kwajalein on 8 March suggests that populations may be greater than indicated by casual observation. This count focused on birds using the northeastern flats at low tide from the Sand's bachelors' quarters to the north point. During this 20-minute count, I recorded 40 Ruddy Turnstone, 12 Lesser Golden-Plovers, and 4 Wandering Tattlers. The tattler proportion (7.1%) of the total was only a little less than the same proportion (9-10%) on the outer islands.

Outer islands may possess relatively higher numbers of Wandering Tattlers than these figures suggest because these islands have more shoreline relative to island area and because the situation in which they were surveyed on Kwajalein would tend to maximize the proportion of tattlers present. Keeping this in mind, I estimate that the number of Wandering Tattlers using Kwajalein Island was probably not less than 25 birds.

GRAY-TAILED TATTLER (*Heteroscelus brevipes*)

The only bird certainly identified as this species during our survey was a bird heard and collected as it fed on the reef just north of Illeginni on 22 March. The specimen was a male that weighed 82 g and had undeveloped testes.

The only other island on Kwajalein Atoll where this species has been recorded is Roi-Namur. Three were collected there 4 November 1964 (Amerson 1969), and Schipper (1985) reported the bird was an uncommon migrant but provided no other details. Schipper's daily tallies indicate that usually no more than two Gray-tailed Tattlers

were seen at Roi. Their occurrence on Roi spans a period from 25 September (1987) to 11 May (1988). Peak numbers were nine on 12 March 1983, and 12 on 1 February 1983. The peak number reported elsewhere in the Marshalls, 10 at Ujelang on 10 February 1977 (Anderson 1981), suggests similar abundance on other atolls.

Even allowing for difficulties in distinguishing this species from the Wandering Tattler, it seems clear that this species is considerably less common than H. incana in the Marshall Islands. To date it has been reported only from Ujelang, Eniwetak, and Kwajalein Atolls, but the Wandering Tattler has been reported from over 80% of the islands and atolls comprising the group (Amerson 1969).

WHIMBREL (Numenius phaeopus)

Whimbrels are widespread migrants and winter residents in the Marshall Islands. They are widespread on Kwajalein Atoll and are considerably more abundant than their congener the Bristle-thighed Curlew. Observations during the March 1988 survey were as follows:

Ennylabagen - An estimated 8-10 birds were present on all visits. The field just northwest of the helipad, which held the largest concentrations of other shorebirds, also had the largest number of Whimbrels with four or five birds seen there on each survey. Whimbrels, like plovers, were widely distributed in open areas, but were even more likely to be found along the shore.

Legan - None seen.

Illeginni - The three to four Whimbrels seen on the two visits foraged along the northern shore and north to the isolated islet.

Roi-Namur - Seven were counted on the first visit to Roi-Namur and nine were counted on the second. As the survey counts missed some of the areas (e.g. near the Altair Radar) where these birds also occur, I estimate the island total was about 12-15 Whimbrels. Most were seen on grassy lawns and fields all over the island, and several were seen resting at the northern lake. A rocky shore exposed at low tide on the western shore of Roi attracted a roosting flock of eight on the afternoon of 26 March (Figure 35).

The only other record of Whimbrels at Roi is one of eight birds that I saw on 4 November 1964 (Amerson 1969). Schipper (1985) mentioned only that it was a common migrant on Kwajalein but provided no more specific details. His notes (in litt.) show that Whimbrels are even more common on Roi than during the March survey. He counted 15 birds or more on 11 occasions. His peak numbers of 24, 27, and 28 birds on 29 September 1988, 8 November 1979, and 20 December 1981, respectively, are the largest numbers recorded at any atoll in the Marshalls. At least a few Whimbrels may be present on Roi-Namur in

Figure 29. Flock of Whimbrels on Roi, 26 March 1988.

every month, but peak numbers are present from early October to mid April (Table 11).

Judged from Schipper's counts, migrants may begin arriving as early as late July. Some continue on to winter on islands farther south.

Gagan - The only bird seen was one that foraged off the northern end of the island on 25 March.

Gellinam - None seen.

Table 11. Numbers of Whimbrels seen by Schipper at Roi-Namur, October 1979-November 1988.

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
1)	5.3	3.7	4.2	4.9	2.0	4.5	3.6	4.4	5.5	5.6	6.0	7.1
2)	17	10	9	14	6	3	9	17	24	16	27	28

(1) Mean number seen per days observed.
(2) Peak number recorded.

Omelek - One was foraging on the rocky flats off the northwest shore on 17 March.

Eniwetak - None seen.

Meck - Most Whimbrels seen here roosted on the north end of the airstrip or foraged in the low vegetation just beyond the airstrip and in the grassy areas of the artificially raised northern end. A few were also seen along the southwestern shore. A maximum of five was seen flying together over the island's northern end and four, later joined by another bird, were together on the north end of the airstrip.

Kwajalein - Perhaps a maximum of eight Whimbrels were present on Kwajalein in March 1988, but usually five or fewer were seen. Earlier records include two seen 19 October 1960 (Fosberg 1966) and an estimated eight present in late October and early November 1964 (Amerson 1969). All were seen in the same areas as on the March 1988 survey.

Whimbrels were seen only on the western portion of the island largely from the southwestern end of the runway west, in March 1988. They foraged in grassy areas but were wary and seldom allowed a close approach. They seemed to prefer roosting in elevated areas. Two or three could be found regularly on the *Cassytha*-infested elevated plateau southwest of the runway, and two were found in the raised dump area on 20 March. Four were together atop a high area being excavated for sand north of Mt. Olympus on 28 March. The maximum number seen at once was five birds roosting on the overrun area on 28 March. Four were on the beach below the plateau on 29 March.

Although Kwajalein possesses much more foraging habitat for Whimbrels than do the other islands visited, the number found is relatively small, perhaps because these birds are more affected by human disturbance on Kwajalein than on Roi-Namur or Ennylabagen.

BRISTLE-THIGHED CURLEW (*Numenius tahitiensis*)

On atolls of the Marshalls where numbers or relative abundance of this species and the Whimbrel have been reported, the curlew is usually reported as less common than the Whimbrel (Anderson 1981, Schipper 1985, this survey). Nonetheless, the Bristle-thighed Curlew has been recorded from far more atolls (24) than the Whimbrel (15), (Amerson 1969, Temme 1990) suggesting that some of the earlier records for *tahitiensis* may well have been of *phaeopus*.

Previous records for Kwajalein Atoll include four seen on Roi-Namur on 4 November 1964 (Amerson 1969) and four seen there on 8 February 1980 (Schipper 1985, in litt.). Schipper (1985) also stated that he saw Bristle-thighed Curlews from Roi-Namur south to Debuu with the majority of sightings at Ennumennet. He gave no specific numbers or dates when curlews were seen at these islands.

Schipper suggested that curlews were most abundant on little-inhabited islands "where a silty ooze collects on the ocean side between the beach and the reef." This assessment of the habitat chosen may reflect more the habitat on the islands visited than the habitat chosen by the curlew. The curlews seen during this survey, and presumably wintering, on Legan and Illeginni were found in distinctly different habitats (see below).

A maximum of five birds were seen during the March survey. One was seen on Kwajalein's raised plateau on 12 March. It was roosting with a Bar-tailed Godwit (Limosa lapponica) but flushed and was not seen again.

Two were seen on Legan on both the 11 March and 24 March visits. On 11 March two flushed from the rubble on the northwestern side and another, possibly one of these two birds, was seen on the interior lake. On 24 March one was seen along the sandy beach on the east side of the island, and another flew into the interor lake to land about 15 feet up a Cassytha-infested Pemphis.

One was seen on both visits to Illeginni. On 14 March one was seen among the rubble on the western side of the isolated north island and on 22 March one was seen between this island and the northern tip of Illeginni.

BLACK-TAILED GODWIT (Limosa limosa)

Schipper saw and photographed two Black-tailed Godwits on Roi-Namur 4 September 1978 (Figure 36) and subsequently saw one to five of these godwits between 25 August and 20 October 1982 (Schipper 1985).

This Palearctic species has been reported widely as a vagrant in Micronesia, but it is more frequently encountered in the westernmost portions (Pratt et al. 1987, Glass et al. 1990). Schipper's records are the only ones for the Marshall Islands and are east of all other tropical Pacific records but one.

HUDSONIAN GODWIT (Limosa haemastica)

A Hudsonian Godwit was seen and photographed on Kwajalein Island in March 1988. It was first seen 11 March as it foraged alone on a lawn southwest of the western taxiway (Clapp and Schipper 1990). The godwit was seen on eight occasions from 11 to 29 March but became wary and was seen less often in late March. It was usually seen where first encountered, but it ranged from the field with the memorial northwest of the runway to the grassy areas just west of the runway's western end. It often used the raised area bordering the ocean for roosting and there associated with Whimbrels and a much larger Bar-tailed Godwit. When flushed, the Hudsonian Godwit sometimes flew with Whimbrels; but if both Whimbrels and the

Figure 36. Black-tailed Godwit on Roi-Namur, September 1978. Photograph by W. L. Schipper.

Bar-tailed Godwit were present, it invariably flew with the latter. When foraging on grassy areas, it usually foraged by itself but occasionally was loosely associated with feeding Ruddy Turnstones and Lesser Golden-Plovers.

Schipper (in litt.) saw another, or possibly the same, Hudsonian Godwit on Kwajalein Island on 8 October 1988 as it fed with a Lesser Yellowlegs and Lesser Golden-Plovers (Clapp and Schipper 1990)

The only prior records of this Nearctic breeder in the tropical Pacific are two sight records from Fiji and one from Oahu, Hawaiian Islands. Australia has one sight record, but the species has been recorded fairly frequently in New Zealand (Clapp and Schipper 1990).

BAR-TAILED GODWIT (Limosa lapponica)

Bar-tailed Godwits occur regularly on Kwajalein but only in very small numbers. Earlier records include one on the southwestern portion of Kwajalein Island on 2 February 1956 (Fosberg 1966) and a male that I collected (USNM 494830) on Roi-Namur on 4 November 1964 (Amerson 1969). Schipper's (1985, in litt.) recent observations show the species is a regular migrant and winter visitor to Kwajalein and Roi-Namur with most present from November to April. Usually, one or

two birds were seen on Roi-Namur; three were seen 1, 16, and 31 January 1980.

These birds have been seen as early as 25 August (1982) and as late as 16 May (1980) and 26 May (1987). These dates are consistent with Stickney's (1943) conjecture that the usual period of occurrence in the tropical Pacific extends from late August to May.

A godwit seen on Roi-Namur on 5 and 7 June and 5 July 1981 presumably was a bird that over-summered. Such over-summering is uncommon but not unknown. Stickney (1943) mentioned nine specimens taken in Fiji on 22 and 23 June and suggested that such birds are largely not yet fully adult.

Two Bar-tailed Godwits were seen during the present survey. One, a large bird seen on the southwestern portion of Kwajalein on several occasions (see Table 6), was probably a female. It seemed to prefer to associate with the Hudsonian Godwit, but sometimes associated with Whimbrels or was found alone. It roosted in the low Cassytha-vegetation on the elevated plateau at the southwest end of the airstrip (Figure 37), but also foraged in grassy lawn just northeast of that area. It once flushed from sandy beach on the perimeter of this area.

Figure 37. Bar-tailed Godwit resting on raised area on Kwajalein Island, 13 March 1988.

The other Bar-tailed Godwit was a breeding-plumaged male seen on Meck Island on 21 March. There it roosted with a concentration of other shorebirds in low vegetation just north of the runway. The bird was very wary and attempts to collect it failed.

This species occurs regularly in small numbers in the Marshall Islands where it has been also reported from Arno, Eniwetak (Amerson 1969), Mejit Island, Bikini (Temme 1990), Majuro and Ujelang Atolls (Anderson 1981). Their period of occurrence in the Marshall Islands spans the dates from 21 October to 20 December (Ujelang) and 3 March (Arno) to 15 April (Ujelang).

RUDDY TURNSTONE (Arenaria interpres)

The Ruddy Turnstone is the most numerous shorebird migrant and winter resident on Kwajalein Atoll and may be regularly expected on any island. Unlike Lesser Golden-Plovers, they usually forage in small flocks and may form large aggregations for short periods. This is reflected in the sometimes great changes in day to day numbers on parts of Kwajalein Island (Table 8).

Kwajalein Atoll, with populations certainly well over 1,000 birds, may hold the largest wintering concentration in the Marshall Islands. This species is also the most abundant shorebird migrant at other atolls, but totals reported elsewhere are not nearly as large. Judged from observations at Roi-Namur (Table 12), some migrants remain as late as early May and others return from the north in July, as indicated by a count of 103 turnstones on 16 July 1987 (Schipper in litt.) Observations from the March 1988 survey are given below.

Ennylabagen - Between 60% and 80% of the 60-75 turnstones were found in and around the helipad and on the field just northwest of it. Small flocks, usually of 4-14 birds, were also frequently encountered in the open areas to both sides of the road north of the helipad. These turnstones were mostly found in open areas of the interor. A few were seen along the shore, and none were found in forested areas or in areas with heavy ground cover.

Legan - Flocks of six and seven birds were foraging in the grassy areas near the helipad on 11 and 24 March, respectively. Flocks of 15 and 10, respectively, were seen on those dates on the interior lake. A few were seen along the sandy and rubble-strewn shores.

Illeginni - On both visits most of the 15-20 turnstones were found along the western shore or on the exposed rocky flats just north of the island. The only birds seen in the interior were three near the helipad on 22 March.

Roi-Namur - Censuses on 26 and 27 March 1988 gave 330 and 276 birds, respectively. Allowing for birds in areas not covered, I estimate the island population was perhaps 375-400 birds. This total

is larger than any recorded by Schipper (Table 12) but is in the same order of magnitude as his larger counts. The only previous estimate is one of 200 made on 4 November 1964 (Amerson 1969).

Table 12. Numbers of Ruddy Turnstones seen by Schipper at Roi-Namur, October 1979-November 1988.

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
1)	58	69	84	87	31	30	33	42	49	41	45	111
2)	273	200	254	264	100	108	103	230	216	216	157	265

(1) Mean number seen per days observed. The sample size for December was only eight which may account for the disproportionately high mean for this month.
(2) Peak number recorded.

Gagan - One was seen at the northern end, another at the southern on 15 March. The single bird seen 24 March was at the northern point.

Gellinam - A flock of eight was seen along the east beach crest and another bird flushed from about 10-12 feet up in a tree on the western side of the Black Noddy colony. The nests in the area from which it flushed were too high for me to check, but turnstones have been noted as egg predators elsewhere in the Marshall Islands (Crossin and Huber 1970) and can be a signicant source of nest loss in European larid colonies (Brearey and Hilden 1985).

Omelek - Five were seen on 17 March along the southeastern shore and five others were on the helipad.

Eniwetak - None seen.

Meck - About 16-20 foraged mostly along shores exposed at low tide. The number seems low for an island this size but may relate to the relatively small amount of grassy area in which to forage. Numbers of other species (plovers, Whimbrels) were relatively much larger and may reflect the greater ease with which these species forage in the low, forb ground cover.

Kwajalein - Counts on Kwajalein reached a maximum of 417 on 23 March, but this total is probably larger than the number actually present in the area surveyed because some birds were very likely counted more than once. Observations suggested that relatively few birds occurred in areas not covered by the census. Taking into account these observations as well as the census data, I estimate the total island population was about 450 birds. The only prior estimate

of numbers during the wintering period is one of 200-300 in October-November 1964 (Amerson 1969).

Substantial concentrations of turnstones formed in the evening and morning on the tarmac outside the aircraft repair shop. There turnstones are regularly fed "Hill's Science Pet Food" and I was informed (W. Dudley pers. comm.) that at least two individuals regularly feed them. Three counts here on the mornings of 23 to 28 March ranged from 123-130 birds with a peak of 210 on the morning of 29 March. The largest foraging group seen elsewhere was one of 102 birds around the Zar transmitter shielding fence on 15 March. Resting birds seem particularly attracted to the sandy parts of the ballfields where a flock of 62 turnstones was seen 29 March.

SANDERLING (*Calidris alba*)

Sanderlings are uncommon migrants at Kwajalein. None was found during the March 1988 survey, but the species has previously been noted at Kwajalein, Roi-Namur (Amerson 1969, Schipper 1985) and Ennumennet Islands (Schipper 1985). Preferred habitat on Kwajalein is exposed sandy areas, few of which were visited during the March survey or by earlier observers. Sanderlings on Kwajalein roost on rocks at high tide (Schipper 1985) and have been found along the airstrip on Kwajalein Island (Amerson 1969).

Usually only one or two birds are seen. The largest numbers recorded on Roi-Namur were three on 23 November 1980 and six on 11 December 1982 (Schipper in litt.). Numbers recorded elsewhere in the Marshall Islands suggest that the species is an uncommon migrant and winter resident throughout the group. The peak numbers reported from other atolls in the Marshalls are seven at Ujelang Atoll (Anderson 1981) and nine at Bikini Atoll (Temme 1990).

Records kept at Roi-Namur (Schipper in litt.) suggest that a few Sanderlings winter there in some years. All but one of the records for Roi-Namur (and Kwajalein) fall between 30 August (1988) and 30 April (1980). A bird seen on Roi-Namur 6 and 9 July 1980 was presumably an early migrant. Observations over a two-year period at Ujelang Atoll (Anderson 1981) reveal a similar pattern with dates of occurrence spanning a period from 28 October to 6 May (both 1976). These dates span all records of this species in the Marshall Islands.

PECTORAL SANDPIPER (*Calidris melanotos*)

The only record of this Nearctic species on Kwajalein is of two seen by Schipper (1985, in litt.) on Roi-Namur. One was present from 20 to 30 October 1982, and one was seen 12 and 19 March 1983 (Figure 2). The only other records for the Marshall Islands are a male (USNM 494814) collected 20 October 1964 on Lojrong Island, Taka Atoll (Amerson 1969), and a bird seen on Enekune Island, Ujelang Atoll from 13 to 24 September 1975 (Anderson 1981).

Pectoral Sandpipers breed in northern North America and on the Arctic coast of central and eastern Siberia (A.O.U. 1983); but in the tropical Pacific they have been recorded regularly only in the Hawaiian Islands (Pratt et al. 1987).

SHARP-TAILED SANDPIPER (Calidris acuminata)

About 25 Sharp-tailed Sandpipers, nine of which were collected, were present on Kwajalein Island in early November 1964 and provided the first record for the atoll (Amerson 1969). More recent observations by Schipper (1985), largely on Roi-Namur, led him to conclude the species is a regular fall migrant. He noted that it arrives in October but provided no other specifics about length of stay or numbers seen.

Schipper (in litt.) has now recorded these sandpipers on Roi-Namur from as early as 26 September to as late as 7 February (both 1982). Peak numbers recorded in 1988 were 30 and 17 on 20 and 31 October, respectively, 22 on 3 and 5 November, and 19 on 11 November. Peaks in earlier years were considerably less: 13 on 20 October 1979, 10 on 18 October 1980, 8 on 23 November 1981, and 11 on 1 November 1982.

Sharp-tailed Sandpipers begin arriving on Roi in late September or early October and peak in late October and early November. This is consistent with observations further to the east in the Phoenix Islands where fall populations also peak in October and November (Clapp and Sibley 1967).

Observations of from 1-7 birds in January and February (Table 13) are probably of late migrants rather than wintering birds. The absence of spring records from Roi may result from spring migrants first reaching Kwajalein Island, stopping briefly there, and then departing the atoll for the north. The buildup of numbers on Kwajalein Island during March 1988 doubtless consisted of migrants arriving from the south, but none was seen on Roi during this period.

Table 13. Numbers of Sharp-tailed Sandpipers seen by Schipper at Roi-Namur, October 1979-November 1988.

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
1)	2.8	1.0	---	---	---	---	---	---	2.3	5.7	5.9	2.8
2)	7	1	-	-	-	-	-	-	4	30	22	5

(1) Mean number seen per days observed.
(3) Peak number recorded.

During the March survey, Sharp-tailed Sandpipers were seen only on Kwajalein Island (Table 6). The first one was seen 13 March as it

fed with 12 Ruddy Turnstones. That I saw no more birds on three subsequent visits suggests that the larger numbers seen later were birds arriving on migration. Ten birds, the largest number seen together, were foraging on 29 March inside the wire fence surrounding the ammunition bunkers near the southwest end of the airstrip. Others were seen on the grassy golf course and at rain pools southwest and north of the runway. When more than one bird was present, the birds flew as a flock. They clearly preferred to associate with flocks of turnstones and seemed to avoid plovers.

After my departure, Schipper (in litt.) recorded Sharp-tailed Sandpipers on four days in 1988: 9 on 2 April, 12 and 7 on 8 and 13 October, respectively, and 6 on 5 November.

Elsewhere in the Marshalls, the Sharp-tailed Sandpiper has been reported from Enewetak (Woodbury 1962, Temme 1990), Jaluit (Amerson 1969) and Ujelang (Anderson 1981), Likiep, and Bikini Atolls and Mejit Island (Temme 1990); but it doubtless occurs more widely. A flock of 64 seen on Enewetak Island, Enewetak Atoll 17 November 1978 (Temme 1990) is by far the largest number seen in the more tropical parts of the Pacific Ocean. The earliest fall records of these sandpipers in the Marshalls are from Kwajalein but they have been seen in spring as late as 16 May at Enewetak Atoll (Amerson 1969).

CURLEW SANDPIPER (*Calidris ferruginea*)

A Curlew Sandpiper observed and collected on Kwajalein Island in March 1988 is the only record for the atoll or for the central tropical Pacific (Clapp and Schipper 1990). The sandpiper was discovered 23 March when it was heard calling as it flew with a flock of Ruddy Turnstones in the field by the battle monument. It was seen again on 25 March as it foraged with turnstones in a grassy area beyond the western end of the runway. I collected it (USNM 596229) on 29 March as it roosted with a flock of Lesser Golden-Plovers on the taxiway. The specimen is a male with unenlarged gonads and was extremely fat, weighing 82 g. The heavy layers of fat suggest that the bird was healthy and would have migrated north in due course.

Curlew Sandpipers breed primarily in northern Siberia (A.O.U. 1983) and winter south to Australia (Condon 1975). They are uncommon migrants in western Micronesia (Pratt et al. 1987). The prior records from the tropical Pacific are two sight records from Oahu, one bird seen and photographed 31 October 1979 (Pyle and Ralph 1980) and another seen 6-23 September 1987 (Pyle 1987).

RUFF (*Philomachus pugnax*)

The Ruff has been noted on Kwajalein Atoll six times. The first bird, presumably a male from its large size, was seen with Lesser Golden-Plovers on the Kwajalein golf course (Temme 1985). Schipper (in litt.) saw another on Kwajalein on 8 and 12 October 1988.

The other Ruffs observed were all seen on Roi-Namur: one from 23 September to 14 October 1979, another from 1 October to 23 November 1980 and on 11 January 1981, a third from 23 September to 1 December 1982, and the fourth, a juvenile, on 28 and 29 September 1988 (Schipper 1985, in litt.)

The Ruff, a species that breeds in the Palearctic, is an uncommon migrant to Hawaii and Micronesia (Pratt et al. 1987) that in recent years has been recorded with greater regularity. In the Marshall Islands it also has been recorded at Enewetak Atoll where a small bird, thought to be a Reeve, was seen on 21 November 1979 at Enewetak Island (Temme 1985). Temme also gives passing mention to a specimen from Enewetak in the USNM. This bird, a Reeve, was collected on Enewetak Island 15 October 1968 (Clapp ms.).

LATHAM'S SNIPE (Gallinago hardwickii)

The only unequivocal record of this Asian species in the Marshall Islands and the tropical Pacific is a male (USNM 494842) collected from a grassy area between the runway and taxiway on Kwajalein Island on 3 November 1964 (Amerson 1969). Temme (1990) reported birds he believed were this species on Aomon Islet, 25 March and 7 April 1979, as well as a less certain sighting of a snipe on Ananij Islet 27 March 1978.

ORIENTAL PRATINCOLE (Glareola maldivarum)

Schipper (1985) saw and photographed an Oriental Pratincole on Roi-Namur following ten days of heavy, southwestern winds. The bird was seen 16 October-11 November 1982 along the southwest lagoon side of the runway where it frequently hawked insects. This species breeds in eastern Asia and is an uncommon migrant in western Micronesia (Pratt et al. 1987). The bird on Kwajalein is the only record for the tropical Pacific east of western Micronesia.

FRANKLIN'S GULL (Larus pipixcan)

A Franklin's Gull was present on the Roi-Namur golf course from 24 June to 3 July 1988. It foraged for grasshoppers and frequented the water catchment basins (Clapp and Schipper 1990). This bird, in first summer plumage, is the second record for the Marshall Islands, the first being a bird in breeding plumage seen on Majuro Atoll on 10 June 1975 (Anderson 1978).

This North American species strays fairly regularly to Hawaii (Clapp, Morgan-Jacobs and Banks 1983, Pratt et al. 1987) and infrequently to Australia (Serventy and Whittell 1976, Eades and Debus 1982, Blakers et al. 1984) and there is one extraordinary sighting from Marion Island, Indian Ocean (Sinclair 1978).

Terns, Sterninae

Tern flocks were seen feeding offshore fairly frequently (Table 14). A few contained only Black Noddies or Black-naped Terns, but most were mixed flocks of the two species. Most of these flocks, and all seen close to islands, contained a fairly small number of birds (4-42 birds, mean 15.3, n: 11). One large flock of about 500 birds was seen off the southern shore of Kwajalein Island on 28 March. This large flock was too far away to determine its composition, but it appeared to consist mainly of Black Noddies and a few white terns (probably Black-naped Terns) and an unknown proportion of larger dark birds, that may have been Brown Noddies (Anous stolidus).

That Brown Noddies and White Terns did not participate in the smaller inshore flocks, even off islands where they breed and are moderately numerous (Illiginni, Legan), suggests that most feed well offshore. Engbring (in litt.) made similar observations in Palau.

Table 14. Size and composition of tern flocks feeding off Kwajalein Atoll in March 1988.

Date/Time		Island	Location	Number of Black Noddies	Number of Black-naped Terns	Number of Crested Terns	Total
10th	0819	Ennylabagen	S of NE point	--	4	--	4
10th	1219	Ennylabagen	mid NE point	10	1	--	11
11th	0830	Legan	rocky N point	6	1	--	7
14th	1409	Illigini	off N shore	6	15	--	21
21st	1000	Meck	off SE shore	10	--	10	10
21st	1018	Meck	off S end	30	12	--	42
21st	1200	Meck	off W shore	--	2	3	5
24th	0949	Legan	off N shore	5	2	--	7
25th	1352	Gagan	off SW tip	15	10	--	25
25th	1506	Gagan	off SW tip	22	9	--	31
26th	0850	Roi-Namur	SW beach of Roi	2	1	2	5

The smaller tern flocks were seen from as close as just off the breakers to as far as perhaps 1.4 mi for one flock feeding south of Meck. The structure of such flocks was tiered, with Black Noddies hovering low (3-10 ft) over the surface and dipping to seize prey while Black-naped Terns arced higher (6-20 ft) and dove into the upper layer of water to catch food.

Great Crested Terns (Sterna bergii) only occasionally fed with these birds. Most Great Crested Terns flew in ones or twos up and down the shores and usually dove from 15 ft or more. This species behaved quite differently in April 1988 at Christmas Island, Pacific Ocean, where it often fed in sizable flocks with Black Noddies. At that locality, where Black-naped Terns are absent, the Great Crested Terns formed the upper tier of the feeding flock, arcing and diving much as did the Black-naped Terns on Kwajalein.

GREAT CRESTED TERN (Sterna bergii)

Great Crested Terns occur throughout the atoll and are frequently seen fishing off the shores of most islands or roosting on sandy points or pilings. They have not been found breeding on Kwajalein, but it seems likely that some nest on isolated beaches on seldom visited islands. They have been reported on northern islands from Nell east through Roi-Namur and south to Gagan (Schipper 1985), and at Kwajalein (Fosberg 1966) and Ebeye (Anderson 1981) Islands.

Earlier data on abundance is largely lacking; the previously reported maxima are six birds at Kwajalein on 29 February 1952 (Fosberg 1966), six at Roi-Namur on 4 November 1964 (Amerson 1969), and five off Ebeye on several occasions in the mid to late 1970's (Anderson 1981).

Crested Terns occur widely in the Marshalls and have been recorded at 22 of the 34 atolls and reef islands comprising the group (Amerson 1969); they are recorded as breeding at eight (Amerson 1969 Anderson 1981). Breeding has been adequately documented for nine atolls. Amerson (1969) indicated Crested Terns breed at another site, Arno Atoll, but the source cited (Marshall 1957) makes no mention of breeding there. Sources cited by Amerson for Crested Terns on Enewetak Atoll also do not mention breeding. Subsequently, however, Anderson (1981) cited native informants who noted breeding at Enewetak. Breeding at Rongelap Atoll is documented by a very young chick (USNM 388733), not much more than a day old. Amerson listed this specimen but questioned whether Crested Terns bred there.

Observations for Kwajalein Atoll are given by island below.

Ennylabagen - None seen on any visit.

Legan - On 11 March, five adults, three in breeding plumage and two in non-breeding plumage, roosted on rubble off the central

eastern shore. This area could supply good nesting sites if it remains exposed at high tide, but no Crested Terns were seen there on 24 March.

Illeginni - A minimum of four birds was seen 14 March and probably at least six were present. One was seen flying along the eastern reef, two were roosting on the sandy beaches on the south side of the isolated island just north of Illeginni, and four more roosted with Black-naped Terns on the northern point of the isolated island. No Crested Terns were seen on 22 March.

Roi-Namur - Four were seen 12 March 1988. Two perched on a concrete piling on the southern side of the island, a third flew overhead, and another flew off the northeast end of the runway. All seen well were in non-breeding plumage. Five, two in juvenal plumage, were roosting on the sandy southwestern point on 26 March. Four others, probably some of the same birds, were on a concrete piling on the south shore the following day (Figure 38).

Schipper (in litt.) typically saw one to four birds off the island's shores (on 244 of 308 days these birds were recorded). Ten or more birds were seen on only 18 days (in over 600), all within the period from 17 March through 22 October. Peak numbers recorded were 41 on 11 September 1988, 35 on 26 May 1987, 23 on 11 May 1987, and 19 on and 15 April 1987. Mean numbers seen per days observed are lower in December and January (Table 15), perhaps reflecting a winter breeding season.

Figure 37. Great Crested and Black-naped Terns roosting on a piling at Roi-Namur, 27 March 1988.

Table 15. Numbers and frequency of occurrence of Great Crested Terns seen by Schipper at Roi-Namur, October 1979-November 1988.

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
1)	1.6	3.0	2.6	3.5	5.8	3.1	2.6	2.8	3.9	3.3	2.7	1.4
2)	2	7	16	19	35	15	9	12	41	12	7	2
3)	7	7	31	25	36	33	41	26	31	46	20	5
4)	.20	.22	.45	.52	.55	.54	.57	.51	.55	.64	.31	.23

(1) Mean number seen per days in which observed.
(2) Peak number recorded during month
(3) Number of days observed
(4) Percentage of days of observation in which seen.

Gagan - On 15 March 16 Crested Terns were seen roosting together on rocks exposed by low tide off the northern point (Figure 39). Nine were seen there on 25 March. On 15 March eleven of the birds were in breeding plumage, three were in transitional or non-breeding plumage, and two were in juvenal plumage. On 23 March

Figure 39. Roosting Great Crested Terns and Black Noddies at the northern end of Gagan Island, 15 March 1988.

four were in breeding plumage, four in non-breeding plumage and one was in juvenal plumage. Thus, a total of at least 18 birds was present on the two visits.

Great Crested Terns also roosted on exposed rocks off the west shore as well as on a large concrete block well inshore. Birds foraged primarily along the western shore. One juvenile was seen pursuing another and begging for food, and one adult was seen making an unsuccessful kleptoparasitic attack on another adult.

At Gagan and Meck, large (6-8 ft) black-tipped sharks (*Carcarhinus melanopterus*) were driving schools of fish toward the shore, resulting in hundreds of small fish leaping into the air within a dozen feet of shore. Great Crested Terns foraging along these shores evidently waited for such events, and flew to such areas and dived repeatedly. Black-naped Terns also utilized shark-driven schools on Meck, but not as frequently as did Crested Terns.

Gellinam - A single bird was seen flying off the western shore in the mid-afternoon.

Omelek - None seen.

Eniwetak - Several Great Crested Terns were flying off the northwesternern shore as we arrived, and an adult and a juvenile were seen off the eastern end shortly thereafter. Later in the morning, an adult was seen returning to feed a juvenile as another adult stood by. All three were on exposed reef rock south of the helipad. When flushed, the juvenile could only fly weakly. No good nesting habitat for these terns is found on Eniwetak; the young bird probably fledged on some nearby island.

Meck - Three, two adults in breeding plumage and a juvenile, constantly patrolled along the sandy beach and breakwater on the southwestern shore.

Kwajalein - One Great Crested Tern flew off the southwestern end of the island on 19 March. These terns may be more common off the ocean side of the island than a single observation suggests because I spent relatively little time on the ocean side. Their absence from the lagoon side where I saw both Black Noddies and Black-naped Terns probably does indicate that the species is a less frequent visitor to Kwajalein than the other terns.

Only a few scattered records document breeding by Great Crested Terns in the Marshall Islands (Table 16), but they are well scattered and suggest either irregular breeding, different breeding seasons in different areas, or perhaps other than an annual breeding regime.

Table 16. Stages of breeding reported for Great Crested Terns in the Marshall Islands (1)

Atoll	Date			Breeding stages observed	Based on observations: Earliest Eggs	Latest Young
Rongelap	31	Jul	1946	small chick collected	24 June	2 Sep
Bikini	19	Aug	1946	small - near-fledging chicks	20 June	21 Aug
	8	Nov	1978	18 eggs, 2 young, ca 2 day & 2 weeks old	12 Aug.	19 Dec
Wotho	11	Sep	1976	6 nestlings	4 July	13 Oct
Taongi	10	Oct	1964	7 eggs	12 Sep.	20 Dec
Bikar	15	Oct	1964	20 eggs, 2 small chicks	2 Sep.	25 Dec
Taka	20-22	Oct	1964	10 eggs	7 Sep.	25 Dec
Jaluit	11	Nov	1964	2 3/4 grown young	16 Sep.	26 Nov
Taongi	29	Apr	1967	49 eggs, two small young	22 Mar.	11 June
Ailinginae	1	May	1967	9 near-fledging young	1 Mar.	11 May
Taka	5	May	1967	1 small young	29 Mar.	7 June
Bikar	7	May	1967	7 eggs	10 Apr.	17 July

(1) Data from Amerson (1969), Anderson (1981), Temme (1990), and USNM specimens. Calculations are conservative estimates; presence of small young suggests at least moderate incubation of other eggs seen. A 28-day incubation period and 43-day fledging period, the latter a maximum (Langham and Hulsman 1986), were used to arrive at the dates given in columns to the right. "Small young" are assumed to be 10 days old, 3/4 grown young 28 days, and near-fledging young 33 days. Eggs are regarded as fresh or incubated, whichever will make the span of possible breeding dates greater.

COMMON TERN (*Sterna hirundo*) or
ARCTIC TERN (*S. paradisaea*)

Anderson (1981) reported a bird he believed was one of these near Ebeye and Kwajalein on 2-4 January 1976. No descriptive details were given, and the bird could have been a winter-plumaged tern of the genus *Chlidonias*. Anderson cites one record each for the Common Tern (Amerson 1969) and Arctic Tern (Woodbury 1962) in the Marshall Islands. The former is a specimen of the nominate race; the latter is a sight record without details that was rejected by both Clapp, Laybourne and Pyle (1983) and by Pyle and Engbring (1985).

BLACK-NAPED TERN (*Sterna sumatrana*)

Previous reports give specific records of Black-naped Terns only on Ebeye (Fosberg 1966), Enebuoj (Amerson 1969), and Gagan (Schipper 1985) despite this species' widespread occurrence on Kwajalein. Black-naped Terns are now known to breed on three islands at Kwajalein. Nests of this ground-nesting bird are not conspicuous and

it is highly likely that the species nests on other islands, particularly those lacking ground predators (dogs, cats, pigs) and that are free from human disturbance.

Judged from available observations it is likely that the total population is at least several hundred birds, but too little of the atoll has been surveyed to allow a conjecture as to the maximum population level. Observations obtained on this survey are given by island below.

Ennylabagen - These terns were seen on visits to this island on 9, 10, and 23 March; but the total number seen was likely no more than half a dozen. On 9 March three birds fed in the lee of the large wrecked ship on the mid-eastern shore. Two were adults and one a juvenile, the latter evidently the offspring of the former as the young bird followed the adults calling continuously. Later, one adult perched with the calling young on the boat itself. Guano on the edge of the ship indicated its regular use as a roost and possibly as a nest-site.

On the following day four were fishing along a Tournefortia edged cove east from the north village. Four birds, presumably these, later flushed from the sandy spit that runs more or less northwest off the north end of the island. The habitat here, at least the more raised, lightly vegetated portion, provides the most likely nesting habitat, but dog and pig tracks on nearby beaches make it highly unlikely that these birds nest here with any success.

Only one was seen on 23 March, a calling juvenile flying along the lagoon side of the south end.

Legan - Two to three Black-naped Terns foraged offshore on both visits. The shores of Legan provide very little potential nesting habitat and I doubt that this tern ever breeds here.

Illeginni - A maximum of 29 birds, all apparently adults, and largely without black carpal bars, roosted on the offshore rocks and sandspit of the island north of Illeginni on 14 March. A flock of about 15-20 birds flew from the raised area of this separated northern island; about 30 birds were also here on 22 March. Although one bird was seen carrying a fish over the island, intensive searching of the areas from which the birds flushed revealed no nests. A male and a female, largely in breeding plumage, that were collected 22 March were molting in the primaries but showed no enlargement of the gonads. Although none were found nesting during this visit, the birds' behaviour, and the nature of the habitat, make it very likely that Black-naped Terns nest on this island.

Roi-Namur - Two were seen on 12 March as they perched with Great Crested Terns on a concrete block near the westernmost of the two piers on the island's south side. An adult and a juvenile perched on a pier railing on 27 March, and another adult was seen on a concrete block on the southern shore.

The presence of Black-naped Terns at Roi-Namur was suggested by Schipper (1985) but he provided no details. His daily tallies indicate that the species occurs there as a visitor throughout the year and is somewhat more abundant in the northern hemisphere winter (Table 17).

Table 17. Numbers of Black-naped Terns seen by Schipper at Roi-Namur, October 1979-November 1988.

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
1)	9.4	4.6	3.8	3.6	3.1	2.4	2.6	1.4	4.0	4.4	3.2	3.8
2)	26	10	17	7	8	6	7	3	12	8	15	9
3)	7	7	18	15	16	13	16	5	11	27	23	5
4)	.20	.17	.26	.31	.24	.21	.22	.10	.19	.38	.36	.23

(1) Mean number seen per days in which observed.
(2) Peak number recorded.
(3) Number of days observed.
(4) Percentage of days of observation in which seen.

Gagan - No Black-naped Terns were found breeding on Gagan during my visits, but Schipper (1985) found six nests with eggs or downy young on 26 August 1979. The nests were on the ground among low vegetation 5 m from the east side of the helipad.

I saw a maximum of six at once on 15 March, and 18 on 25 March. The largest numbers roosted on small rocks off the northernern point, but the southwestern sandspit was also used frequently. Its shallow slope led these birds to use it as a bathing area. Bathing birds walked to the water's edge and then out into it, eventually to be carried off their feet by the waves.

None of the birds seen was a juvenile. Approximately 80% of the birds showed dark carpal bars, possibly a sign of non-breeding status. No nests were found, nor did any of the birds behave aggressively. The island provides adequate nesting habitat, however, and nesting there at other times of year seems likely.

Gellinam - Birds were initially seen around the island perimeter, roosting on rubble and usually in twos. Later, nine were seen together on the western beach, and a maximum of 13 was flushed from the northwestern area. Most were adults, with and without black carpal bars, but one begging juvenile accompanied by a bird with a black carpal bar was seen. I found no nests, nor did the birds' behavior strongly suggest breeding. Ken Jourdan (pers. comm.) told me that a total of about 18 pairs nested on Gellinam around January - March 1986. Undated photographs provided by Jourdan show numerous

eggs and small chicks as well as a few near-fledging young.

Omelek - At least six Black-naped Terns were present, all adults lacking dark carpal bars. Three roosted on the southwestern point and two more on the northern point. Black-naped Terns were much more demonstrative on Gagan than any other island except Meck (where a nest was found). Calling, they flew above me to investigate my presence. I found none of their rather cryptic nests but think it likely that the species nests here.

Eniwetak - Two were seen on the southeastern reef flat, one in pronounced juvenal plumage.

Meck - Ten Black-naped Terns roosted in medium rubble at the southeastern corner of the runway when we arrived. They showed no particular attachment to the island when flushed, but others seen farther north were more aggressive than birds anywhere else. After much searching, I found a nest with an egg and a newly hatched young on a flat rock on the beach crest a little more than one-third the way up the island's east side (Figures 40, 41). I was struck in the head three times by an adult at this point, presumably one of the parents. A very careful search of this area revealed no more nests.

Figure 40. Black-necked Tern chick and egg, Meck Island, 21 March 1988.

Figure 41. Nesting habitat of Black-naped Terns on Meck Island, 21 March 1988.

Kwajalein - F've were seen along the lagoon side of the northeastern portion of the island on 19 March: an adult followed by a calling juvenile, another adult flying alone, another seen foraging, and one perched on a buoy not far from shore.

LITTLE TERN (Sterna albifrons)

The only report of this Old World species on Kwajalein was of a bird seen on southeastern Roi-Namur on 26 July 1981 (Schipper 1985) where it foraged over the reef. This white-tailed species was only recently (A.O.U. 1983) separated from the similar New World Least Tern (Sterna antillarum) which has a gray tail and distinctive vocalizations (Pratt et al. 1987).

Earlier sight records of both species usually failed to provide enough descriptive detail to allow their subsequent identification. Some of the records for albifrons accepted by Pratt et al. (1987) such as those for Upolu, western Samoa, and Ocean Island (Banaba), are equivocal as are virtually all of the records of antillarum from Hawaii (Clapp 1989b). Schipper's record for Kwajalein is one of the very few where the observer provided details that allow the species to be determined.

SOOTY TERN (Sterna fuscata)

Few reports document the occurrence of this abundant tropical seabird at Kwajalein Atoll. A report of "2 Sooty Terns... or Gray-backed Terns (Sterna lunata) along the beach at Kwajalein" in late July 1960 (Yocum 1964) was accepted by Amerson (1969) as a record for both species; but it should have been discarded. Fosberg (1966) reported that one was seen at Eniwetak on 23 January 1952, but no details are available and the record is equivocal. All other records for Kwajalein are provided by Schipper (1985), who saw five adults, one in the lagoon to the east of Gehh Island and the others in different years off the shores of Roi-Namur. He also found a dead juvenile on the western side of Roi-Namur. Dates were provided for none of these observations.

More recently, Schipper (in litt.) has recorded Sooty Terns off Roi-Namur on four occasions: two on 15 March 1983, 23 on 24 May 1987 and one the following day, and one on 13 March 1988.

BROWN NODDY (Anous stolidus)

Brown Noddies are common on Kwajalein but are by no means as abundant as the smaller Black Noddy. They seldom forage inshore and are seen regularly only on islands where they breed. They have been sighted previously at Kwajalein (Baker 1951, Temme 1990), Lojjairok, Enubuj, Eniwetak, Ennylabagen (Fosberg 1966), and Loi islands (Fosberg 1966, Amerson 1969). Schipper (1985) reported that the species breeds at Obella, Edgigen, Debuu, Edjell, and Gagan; but he provided no details and Fosberg (1966) reported evidence of breeding at Loi and/or Lojjairok. Observations of this species at other islands are summarized below.

Ennylabagen - The only previous record of Brown Noddies at Ennylabagen was a bird seen flying just offshore on 3 August 1952 (Fosberg 1966). I saw 3-5 Brown Noddies flying over the southern end of the island on 10 March and two flying over the island on 23 March. One of the birds seen 10 March was flying low among Pandanus on the southwest part of the island. Although I found no nests, a few pairs may breed here. The forested parts of the island provide such an abundance of nest sites that Brown Noddies could probably nest successfully despite the presence of native Marshallese.

Legan - Perhaps 30 pairs of Brown Noddies breed on Legan and the total population is probably on the order of 80 birds. I first found nests there on 23 March. Five of the six nests found were at the base of Cocos fronds, and the remaining nest was on a Pandanus leaf (Figure 42). Nests were about 17-25 feet up. An eggshell was found on the ground near one of the nests in Cocos. The nest in Pandanus was discovered when the medium to large downy chick it contained was heard calling to its parents. This nest was on the northeastern part of the island; the others were all in the east-central portion north of the open observation shed. Behavior of other Brown Noddies suggested that additional nests were present, some in Cocos and some in Pandanus, at sites that could not be seen from the ground.

Illeginni - At least five active nests were present, four in Cocos in the central portion of the island and west of the road. The other nest was in the top of a 45-foot Pandanus on the southeastern part of the island, just south of the southeastern corner of the artificially raised area. Most nests were high in the trees with none lower than 20 feet. Examination of smaller Cocos near the pier revealed no evidence of nests. A medium-sized downy young was seen in the nest in Pandanus, and several of the birds perched on palm fronds were immatures. A few other nests probably were present in the taller Cocos and Pandanus. The breeding population is probably not less than 10 pairs.

Figure 42. Brown Noddy nest in Pandanus, Legan Island, 24 March 1988.

Roi-Namur - One Brown Noddy flying over the east end of Namur on 26 March was the only bird seen during the March survey. No other reports put this species at Roi-Namur, but Schipper (in litt.) has seen it offshore in all months of the year. Flocks of 100 birds or more have been seen on 11 occasion, more than half in May and June.

Gagan - None seen.

Gellinam - None seen.

Omelek - One Brown Noddy flew over the west side of Gagan on 17 March. I have no reason to believe that any breed there.

Eniwetak - Perhaps 10-15 Brown Noddies were on Eniwetak, one of them a fledged juvenile perched high in a *Pisonia* tree that also supported a large Black Noddy colony. The others were seen occasionally in the upper canopy and flying along the outer reef. I found no nests but think a few pairs likely nest on Eniwetak.

Meck - None seen.

Loi - About 20 Brown Noddies were flying over the island and roosting in *Pisonia* when I visited the island in November 1964 (Amerson 1969). The species probably nests there in at least small numbers.

Kwajalein - The only birds I saw were about 100 flying southwest, singly and in pairs, off the western end in the late afternoon of 29 March. The birds streaming past were both Black and Brown Noddies and I estimate an aggregate total of 250 birds.

BLACK NODDY (*Anous minutus*)

Black Noddies are one of the most familiar sights of Kwajalein Atoll and are its most abundant breeding bird. Despite its abundance, the species has been recorded breeding on only Eniwetak (Fosberg 1966), Obella, Edgigen, Debuu, Edjell, and Gagan (Schipper 1985) islands. The occurrence of Black Noddies has also been reported from Lojjaiong, Kwajalein, Loi, Ebeye, and Roi-Namur islands (Fosberg 1966, Amerson 1969). Previous data on numbers are few and inexact, but hundreds were said to be nesting on Eniwetak on 23 January 1952 (Fosberg 1966). Data from the present survey are given by island below.

Ennylabagen - Black Noddies only visit Ennylabagen; about 15 were present on 10 March. Three noddies roosted in an open *Pisonia* tree in the central portion of the island on 23 March. A dead bird found 10 March had evidently collided with one of the antennae wires. It had a well developed brood patch suggesting that it was nesting somewhere nearby.

Legan - Fourteen nests were found during the two days I spent on Legan, but at least one nest was inactive. Almost all nests found had sitting birds, and I estimate that there were 12 breeding pairs. Nine of the nests were 60 ft up in two adjacent Pisonia trees on the northern portion of the island. Two others were about 15 ft up in Pemphis, two were about 12 ft up in Tournefortia near the north beach crest, and one was 5 ft up on a low branch of Pisonia. The latter nest, the only one low enough to be examined, contained an incubated egg. The consistency with which adults sat on other nests suggests that most had eggs or very small young.

Illeginni - Forty-seven nests were found in Pisonia, Tournefortia, and Coccoloba north of the trailers on the southern and western portion of the island. Allowing for inactive nests, I estimate the breeding population at about 40 pairs and at least 100 birds. All nests were 20 ft or more above the ground; the majority were at heights of 30 to 40 ft. The behavior of the nesting birds suggested that either eggs or small young were present.

Roi-Namur - A few were flying offshore on both visits, but the Black Noddy does not breed on Roi-Namur. Two were using the understory of the western pier at a perch from which to fish on 26 March. Large flocks of 100-300 birds were seen off Roi-Namur on 19 different days during 1979-83 and 1987-88 (Schipper, in litt.). Seven of these flocks were seen in May 1987 and four in July 1987.

Gagan - Three Black Noddies flew over the grove at the southern end on 14 March, and three roosted on the southwest triangle of sand with Black-naped Terns on the 25th. Schipper (1985) found Black Noddies nesting on Gagan but provided no details. The open Pisonia forest of the northern end that formerly held their nests (Schipper, pers. comm.) now has no nesting birds nor were there any old nests.

Gellinam - A substantial colony of Black Noddies nests in Pisonia forest at the northern end of Gellinam (Figure 43). I counted 266 nests; and allowing for inactive nests, I place the breeding population at about 225 pairs.

Gellinam is the only island visited during this survey where Black Noddies nest low enough so I could examine the contents of a reasonable sample of nests. They were placed from as low as 4 ft to as high as about 40 ft with the majority from 15 to 30 ft.

Of nests with contents that could be seen, 8 were empty, 12 contained eggs, and 18 held young. These figures overestimate the proportion of young present because young could be seen in higher nests where eggs could not. Probably not less than 60%, perhaps more, of the active nests contained eggs. Five eggs candled were uniformly heavily incubated, and most of the young were quite small and less than a month old. Two to three large young were seen, one of which was capable of weak flight.

Figure 43. Gellinam Black Noddy colony from east end of grove, 16 March 1988.

Omelek - An estimated four pairs and a total of 15 birds was present. Four active nests and three inactive nests were found in the mid-eastern portion of the island. Nests were too high (ca. 25 ft) to check the contents, but the birds sat tight as on Legan and Illeginni so it seems reasonable to suppose that most contained eggs or small young.

Eniwetak - This island contains a burgeoning population of nesting Black Noddies - one that contains well over twice as many nesting pairs as all other islands visited combined. I counted 1,163 nests on 18 March but estimate the number of active nests at 750, the population at about 2,000 birds. These noddies nest throughout the Pisonia forest which is the oldest and largest such forest encountered during our survey.

Nests were at heights from 20 to 80 ft with most 60 ft or more (Figure 44). A few young were seen, and many adults were sitting on nests suggesting that the stage of breeding, not much different from that found on Gellinam, was fairly evenly divided between eggs and chicks.

Figure 44. Colony of Black Noddies on north end of Eniwetak Island, 18 March 1988.

In two areas the Pisonia were fruiting and their small sticky seeds formed a carpet several inches deep beneath the trees. These seeds were a hazard to both Black Noddies and White Terns because they gummed the feathers when the birds flew into the trees, often causing the terns to fall to the forest floor (Figure 45) where they died of slow starvation. I found a total of 13 Black Noddies and seven White Terns on the forest floor. Five of the Black Noddies and one of the White Terns were still alive; the others had succumbed.

Figure 45. Black Noddy entangled in *Pisonia* fruit, Eniwetak Island.

Meck - The Black Noddy visits this nearly denuded island in small numbers. One roosted on a piling along the southwestern shore, and others were feeding offshore. No nests were found, and the species probably does not nest here.

Kwajalein - These terns only visit Kwajalein but were regularly seen along the perimeter of the lagoon at the northeastern portion of the island. Here, Black Noddies either foraged along the shores or perched on buoys. Only one to three were seen at any time.

WHITE TERN (*Gygis alba*)

This tern occurs in small to moderate numbers on most of the islands, but very little has been said of its numbers or its breeding status. It has been recorded previously at Kwajalein, Loi (Fosberg 1966, Amerson 1969) and Enubuj Islands (Fosberg 1966); and it has been found breeding on Eniwetak (Fosberg 1966), Roi-Namur, Ennumennett, Obella, Edigen, Debuu, Edjell, and Gagan Islands (Schippper 1985). During the March 1988 survey, it also was found nesting on Kwajalein and Legan Islands; and it probably breeds on other islands visited (e.g. Ennylabagen, Gellinam, Omelek). Observations are given by island below.

Ennylabagen - A total of 15-20 White Terns was seen during our visits to Ennylabagen. No nests were found but this species probably nests there in small numbers. Breeding was strongly suggested by one tern with a fish in its bill that landed near another in Pemphis along the island's southeastern perimeter. White Terns occur primarily in the southern third of Ennylabagen where a maximum of seven were seen in flight at once. Others perched in Pisonia in the south-central portion. Only five were seen in the northern part of the island: three flying over a small antenna field along the northeastern perimeter and two, presumably a pair, showing interest in a Coccoloba in shrubby forest at the north end.

Legan - Legan holds the largest nesting concentration of any island visited. Five nests, two with eggs and one each with small downy young, large downy young, and a near-fledging immature, were found. I estimate that not less than 25 breeding pairs and perhaps 75 birds were present. I base this on the difficulty of finding nests and on maximum counts of 15 birds seen at once in the air along the northeastern perimeter on 11 March and 18 over the central lake on 24 March.

Eggs were found in the hollow top of a small Pisonia stub four ft tall (Figure 46) and 12 ft up on a horizontal branch of Pemphis

Figure 46. White Tern nest site on Pisonia stub in open Pisonia forest at the north end of Legan, 11 March 1988. Arrow points to egg.

(Figure 47). The downy chicks were found at heights of 6-7 feet in live and dead Pemphis and the near-fledging chick was on a Pisonia branch 10 ft above the ground. Four nests were on the island's northern end, and one was between the shed on the eastern side and the central lake. Legan's White Terns occur primarily east of the lake and in the northern part of the island in Pisonia forest and in fringing Pemphis. Only two to three White Terns were seen in the southeastern fringe of forest, and they were absent from the understory along the western perimeter and in the open coconut forest north of the lake.

Eller - Although flyovers of largely unidentified islands along the atoll perimeter revealed that White Terns are widespread, the number seen over Eller (at least 30 on 12 and 14 March) suggests that this island holds one of the largest concentrations on the atoll.

Illeginni - Small numbers flew along the perimeter on 14 and 22 March. A maximum of three was seen over a Black Noddy colony at the southern end. White Terns were less common on Illeginni than I would have thought from the habitat available, and I doubt if more than two or three pairs were nesting there in March.

Gae - Small numbers (10 birds or so) were seen from the air during our survey. A local informant stated that White Terns nest there in some numbers.

Figure 47. White Tern nest site on horizontal limb of Pemphis, Legan, 11 March 1988. Arrow points to egg.

Roi-Namur - White Terns are uncommon on Roi-Namur where they occur almost exclusively in the heavily vegetated northern portion of the island and in trees near the airport. About eight were present in March 1988 which compares favorably with an estimate of 10 made during my visit to the island on 2 November 1964 (Amerson 1969). A chick less than a week old was at about 25 ft on the branch of an _Artocarpus_ on 13 March. Schipper (1985) stated that other nests on Roi-Namur have been found in _Artocarpus_, _Pandanus_, and _Pisonia_.

Gagan - A maximum of six birds flew over the southern forest on 25 March. Others, or perhaps the same birds later, flew over the northern forest. I found no nests and all White Terns left the island at midday, which suggests that active nests were not present. A photograph taken by Schipper on 26 August 1979 shows chicks less than a week old.

Gellinam - Four White Terns were consistently present in the Black Noddy colony at island's northern end. No nests were found, but a few pairs likely breed on Gellinam.

Omelek - A maximum of seven birds was seen on 17 March. Six were adults and one was a late juvenile that could fly well but that retained traces of the flecking characteristic of the juvenal plumage. Birds flew over the forest at the north end and along the southeastern shore.

Eniwetak - Fosberg (1966) reported that large numbers were present on 19 January 1952 and noted the presence of several young. White Terns were not numerous on 18 March 1988, when perhaps 20 flew about the upper story of the _Pisonia_ forest. Others were found dead and alive entangled in the carpet of fruit beneath some of these trees. I saw no evidence of nesting but have no doubt that White Terns breed on Eniwetak and that some were breeding during our visit.

Meck - I saw no White Terns on Meck, and they probably occur there only as a casual visitor.

Loi - I estimated that 30 were present on Loi on 8 November 1964 (Amerson 1969). At that time birds were roosting in _Pisonia_ and probably nested there.

Kwajalein - Kwajalein has a population of about 10 White Terns, all associated with trees north of the ball fields north through the residential sections to about the high school. One bird was seen on a nest 40 ft up a _Casuarina_, and several other terns acted as if they were mated pairs.

FORK-TAILED SWIFT (_Apus pacificus_)

Schipper (1985) found one to three of these birds on the southwestern end of Roi-Namur from 31 October to 7 November 1982. The only other reports from the tropical Pacific of this vagrant from

the western Palearctic are two fall sight records from Saipan in the Northern Marianas (T. K. Pratt *in* Pratt et al. 1987) and a specimen collected at sea in the northern Marshall Islands (Clapp 1989a).

SACRED KINGFISHER (*Halcyon sancta*)

One of these birds was seen irregularly from 5 April to 22 August 1981 on the chicken farm on western Roi Island (Schipper 1985, in litt.). A second bird was seen there 11 July. Both birds usually perched well within a Beach Heliotrope (*Tournefortia argentea*) tree. Sacred Kingfishers are common in the southwest Pacific and breed in Australia, New Zealand, and New Caledonia. They migrate north after breeding (Pratt et al. 1987). Schipper (1985) concluded that the birds on Roi-Namur were migrants that overshot their wintering range.

COMMON MYNA (*Acridotheres tristis*)

The Common Myna is an abundant resident in the main Hawaiian Islands and also has been introduced successfully to the Fiji, Cook, Society, and Marquesas islands (Pratt et al. 1987). They were briefly present on Kwajalein Island during the early 1950's. Marshall (1957) reported one on the main airport building 11 June 1950. At least several pairs were present from mid January to mid March 1952 (Fosberg 1966). About a half-dozen were seen eating papayas (*Carica papaya*) in July 1956 (Marshall 1957). Fosberg (1966) saw none in February 1956, however, and failed to find any during visits in 1958 and 1960.

HOUSE SPARROW (*Passer domesticus*)

A maximum of three House Sparrows was seen on Kwajalein Island during a survey in October and November 1964. Sparrows were seen flying in and around the fuel depot-docking and nursery areas, but no details were provided by Amerson (1969). The lack of details may have led Pratt et al. (1987) to suggest that these birds were misidentified Eurasian Tree Sparrows. I did not take part in the attempts to mist net the birds mentioned by Amerson, but I did see one female-plumaged bird and heard the distinctive call. I have no doubt that they were House Sparrows that soon died out.

EURASIAN TREE SPARROW (*Passer montanus*)

This introduced passerine is a common resident of Kwajalein Island that appears to be becoming gradually more abundant. The first observation of what was presumably this species occurred when Anderson (1981) reported 20 unidentified *Passer* on Kwajalein on 1 March 1977. Several birds were identified as Eurasian Tree Sparrows during October 1978 (K. Guthrie *in* Engbring and Owen 1981, Temme

1985). Schipper (1985, in litt.) recorded this species from the Pacific Bachelor's Quarters and the Pacific Ding Room (about a third of the way up the east side of the island) south to the nursery during visits from October 1979 to February 1983. He regarded them as particularly abundant near the Chapel and Richardson Theatre. The largest numbers of sparrows recorded by Schipper (in litt.) were 34 on 20 August 1980 and 40 on 24 October 1981 and 21 August 1982.

In March 1988 I found this sparrow locally common not only in the areas recorded by Schipper but also north to Sand's bachelor's quarters and south throughout the eastern portion of the island to the terminal and aircraft repair shop, in the area with buildings along the lagoon side of the island, and west to the northwestern end of the runway. Flocks of birds also frequently foraged on the raised area west of the runway and in grassy areas along the runway and in the golf course from the southwestern end of the runway to about two-thirds of the way from the runway's northeastern end. The only areas in which these birds were not seen were the northern portion of the residential area on the northeastern part of the island and at the eastern end of the runway.

The largest number of birds that I saw on any one day was about 50 on 2 March, but on that day I covered less than half the area the birds are known to inhabit. I can estimate the population with no great certainty; but incidental observations, made for the most part during shorebird surveys, suggest that the population cannot be less than 200 individuals and may be as high as 500.

These birds feed largely on weed seeds, judged from the frequency with which flocks were found in the grassy areas. Birds also came to the terminal to feed on pet food put out for the turnstones (Figure 48). Sparrows were present near stores but did not display the avid tendency to scavenge characteristic of the closely related House Sparrow. They were also much warier than that species and seldom allowed an approach as close as 15 ft. They were also drawn to air-conditioners, the condensation from which appears to be their primary source of fresh water.

Figure 48. Eurasian Tree Sparrows feeding on pet food, Kwajalein, 29 March 1988.

I found no nests, but observed two birds copulating near warehouses at the runway's western end. The preference of these birds for both open sheds and for coconut palms leads me to believe that these may be breeding sites. The palms seem particularly attractive to the sparrows as they were frequently seen spiraling upwards 60 ft or more to reach the fronds.

The source of these birds is unknown, but the species was known from the tropical Pacific only from the Mariana Islands prior to its occurrence on Kwajalein (Pratt et al. 1987). They may have arrived at Kwajalein on a flight from Guam where these birds are common around the terminal.

Other vertebrates

Despite carefully surverying the shores of the eight outer islands, I found no evidence of previous nesting by Green Turtles (Chelonia japonica). A Green Turtle with a 15 inch carapace that was captured offshore Gagan Island was the only turtle seen during this survey, but I was told by Schipper that two Hawksbill Turtles (Eretmochelys imbricata) with carapaces about 18 inches long were currently being seen off the old Jackaroo Club building on Roi-Namur.

He also stated that both species were formerly much more abundant off Roi-Namur. In 1978 as many as nine Green and Hawksbill turtles could be seen at once. Populations are said to have been depleted by an increase in the rate of capture for barbecue parties. Breeding by the Green Turtle has been alleged but no substantive information is available. Of the islands visited Ennylabagen had what I regarded as the best nesting beaches, but the numbers of inhabitants and burgeoning populations of introduced animals make it very unlikely that any breed there now.

The only reptile previously reported to occur at Kwajalein is the House Gecko, Hemidactylus frenatus (Crombie, ms.); but at least several other species of lizard occur there. I noted lizards only on Ennylabagen, Illeginni, and Gegan Islands; but Herbst reported seeing a small lizard on Eniwetak Island, and Fosberg (field notes) saw them there in 1952. I found old gecko eggs in trees on Meck and Kwajalein. I am not sure what species they represented, but they looked much like those of the Mourning Gecko (Lepidodactylus lugubris), that I have seen elsewhere in the Pacific and that is likely to occur on Kwajalein.

Most of the lizards seen appeared to be Azure-tailed Skinks (Emoia cyanura), but a large Green Tree Skink (Lamprolepis smaragdina) was seen in a tree along the southeast shore of Ennylabagen. Schipper (pers. comm.) informed me that a few of these lizards also occur on the northeastern portion of Kwajalein Island, but I found none there during my visit.

Small lizards were most abundant on Ennylabagen where they were moderately abundant in palm fronds on the forest floor. I only saw

one or two lizards along the eastern shore of Illeginni and on the forest floor of southern Gagan.

I saw Polynesian Rats (*Rattus exulans*) only on Illeginni (one near the helipad) and on Namur (several in forested areas), but I have no doubt that they are more widespread. Rats of one species or another have also been seen on Eniwetak (Fosberg, field notes) and it seems likely that the Norway Rat (*R. norvegicus*) or the Black Rat (*R. ratt*[illegible] [illegible]rs on more developed islands such as Kwajalein, Meck, and Illeginni.

Introduced domestic animals inhabit several islands, with cats especially numerous on Roi. Cats and dogs are common on Roi-Namur, Kwajalein, and Ennylabagen. A cat was seen near the security trailer on Gagan, and a pair was present on Illeginni. I was informed that litters of the latter are destroyed to reduce the probability of establishing a feral population. Ennylabagen also has numerous chickens and pigs; as many as 10 of the latter were seen at once.

Discussion

Previous environmental disturbance of most islands visited was so extreme that I believe breeding populations of seabirds are no more than a small fraction of their former numbers. Loss of nesting habitat for indigenous terns and boobies on Kwajalein, Roi-Namur, Ennylabagen, and Meck islands has resulted from clearing for buildings, runways, helipads, antennae fields, and other structures and has surely much reduced bird populations. Shorebird populations, on the other hand, may have benefited from the increased area available for foraging and resting.

During the March survey, I found evidence of human predation on seabirds on two occasions. A pair of Black Noddy primaries was found tied together by their tips near the security trailer on Omelek, and several pairs of White Tern primaries were found in similar condition near the open shed on western Legan. The effect of such depredations is probably minimized by the presence of security personnel on the various islands.

Two islands are of particular importance to breeding bird populations on Kwajalein and would best be left undisturbed. Legan, with its central lake unique among the islands visited, provides a valuable resource for shorebirds; and the vigorous *Pisonia* forest at the island's northern end has most of the nesting White Terns found on the March survey. Legan also has a small Black Noddy population and the largest nesting Brown Noddy population of any island visited. Eniwetak Island has the largest and best developed *Pisonia* forest, and its large Black Noddy colony dwarfs those elsewhere. Eniwetak has been an important nesting area for these noddies for over 30 years and may be the primary breeding area on the entire atoll.

The Black Noddy colony on Gellinam is also worth preserving. Illeginni, despite considerable environmental manipulation, has shorebird and tern nesting habitat worth preserving.

Even though Ennylabagen has more remaining forest than any island but Legan and Eniwetak, tern populations there are far less than I would have expected from the amount of habitat available. Presumably, native populations and burgeoning populations of introduced animals have already much reduced bird populations.

The other islands visited -- Omelek, Meck, Kwajalein, Roi-Namur, and Gagan -- have so little remaining habitat of value to resident seabirds that further development will have no significant effect.

Summary

Fifty-four species of birds are now known from Kwajalein Atoll, This is due largely to intensive observations by William L. Schipper during the 1980's. This is the largest faunal list for any of the oceanic atolls in the central Pacific except for Laysan Island, in the Northwestern Hawaiian Islands. Most of the avifauna (42 species) consists of vagrants, migrants and transients. A small resident component includes eight native seabirds, one heron, and an introduced sparrow. Two other introduced passerines no longer occur.

Native bird populations on Kwajalein have probably been much reduced as a result of habitat modification, but this change has apparently allowed a substantial increase in wintering shorebird populations. Of the islands examined during the March survey, only four -- Gellinam, Illeginni, Legan, and Enewetak -- possess substantial nesting seabird populations.

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Appendix Table 1. Bird populations on islands of Kwajalein Atoll in March 1988.[1]

Species/Island:	ENN	LEG	ILL	R-N	GAG	GEL	OME	ENI	MEC	KWA	Totals
Red-tailed Tropicbird	-	-	-	-	-	-	1	-	-	-	1
Red-footed Booby	-	-	-	1	-	-	-	-	-	-	1
Great Frigatebird	1	2	-	2	-	-	-	2	-	1	8
Pacific Reef Heron	5	4	6	4	2	-	1	-	-	3	24
Lesser Golden Plover	100	20	25	230	5	4	1	3	60	270	718
Wandering Tattler	20	10	10	30	1	1	2	1	1	25	101
Gray-tailed Tattler	-	-	1	-	-	-	-	-	-	-	1
Whimbrel	10	-	4	15	1	-	1	-	7	8	46
Bristle-thighed Curlew	-	2	1	-	-	-	-	-	-	1	4
Hudsonian Godwit	-	-	-	-	-	-	-	-	-	1	1
Bar-tailed Godwit	-	-	-	-	-	-	-	-	1	1	2
Ruddy Turnstone	75	25	20	400	2	9	10	-	20	450	1011
Sharp-tailed Sandpiper	-	-	-	-	-	-	-	-	-	-	13
Curlew Sandpiper	-	-	-	-	-	-	-	-	-	1	1
Shorebird subtotals	205	57	61	675	9	14	14	4	89	770	1898
Great Crested Tern	1	5	6	4	18	1	-	5	3	1	43
Black-naped Tern	6	3	30	2	10	15	6	2	12	5	91
Brown Noddy	5	80	30	1	-	-	1	15	-	-	132
Black Noddy	15	30	100	5	3	500	15	2000	5	5	2678
White Tern	20	75	10	8	6	4	7	20	-	10	160
Eurasian Tree Sparrow	-	-	-	-	-	-	-	-	-	200	200
Totals	257	256	243	702	48	534	45	2048	109	995	5237

Island:	ENN	LEG	ILL	R-N	GAG	GEL	OME	ENI	MEC	KWA
Birds/acre[2]	2.07	14.22	7.84	1.76	8.00	106.80	5.62	136.53	1.98	1.32
Shore-birds/acre	1.65	3.17	1.97	1.70	1.50	2.80	1.75	0.22	1.62	1.03
Terns/acre	.37	10.72	5.68	.03	6.17	104.20	3.62	136.44	0.54	.03

1) Estimates are maxima. ENN: Ennylabagen, LEG: Legan, ILL: Illeginni, R-N: Roi-Namur, GAG: Gagen, GEL: Gellinam, OME: Omelek, ENI: Eniwetak, MEC: Meck, KWA: Kwajalein.

2) These figures are not rigorous density estimates, but hopefully will provide a rough index of the relative wildlife values of each island. Figures for terns and shorebirds suggest varying values as wintering grounds for migrants and as nesting areas for seabirds, respectively.

Appendix Table 2. Number of days on which William Schipper listed observations on Roi-Namur*.

	Month												
Year:	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	TOTAL
1979										10	2	7	19
1980	15	11	11	7	14	7	15	5	7	14	10	-	116
1981	2	-	4	6	7	8	15	6	-	11	13	2	74
1982	5	8	4	2	4	1	-	4	11	16	9	3	67
1983	6	11	19	6									42
1987	-	2	7	17	18	17	15	9	12	-	18	10	125
1988	7	7	24	10	23	28	27	27	26	21	11		211
Totals	35	39	69	48	66	61	72	51	56	72	63	22	654

*Data sheets for September 1981 and July 1982 are unavailable. Schipper was in Australia in October 1987.

Appendix Table 3. Approximate times that shorebirds were censused on different parts of Kwajalein Island.

	Times of observation on March:[1]							
Area/Date	17	20	23	24	25	28	28	29
Golf course (2)			1710	1712	1748	0822	1615	0930
Runway margin (3)			1710	1712	1748	0822	1615	0930
Stop sign to Mt. Olympus (4)		0920	1740	1735	1730	0810	1555	0915
Plateau (5)	0910					0755	1548	0905
Battle memorial field (6)	1740	0900	1750	1745	1720	1740	1540	0855
Fields N of Mt. Olympus (7)	1740	0900	1750	1745	1720	1740	1540	0855
"Dump road" field (8)	1730	0850	1755	1750	1715	0735	1540	0850
N to Coral Sands (9)			1800	1755	1710	0730	1535	0845
Coral sands to helipad (10)	1715		1810	1805	1700	0725	1530	0840
"O" field (11)	1715		1815	1815	1650	0725	1530	0840
Helipad field (13)			1820	1825	1645	0720	1525	0835
Helipad to aircraft shop (14)			1825	1830	1640	0715	1520	0825

1) For larger areas censused over longer periods of time (20 minutes or more for the golf course) the midpoint of the observation time is given.
(2) Grassy area along the south side of the runway.
(3) Area south of the runway from its eastern to western ends.
(4) Both sides of the road from the easternmost stop sign at the west end of the runway to the access road to the western corner of the northwestern extension of the runway and to the base f the elevated area southwest of this extension.
(5) The elevated area beyond the west end of the runway and southwest of the northwestern extension of the runway.
(6) East of Olympus Drive and west of the northwest runway extension to a point where a road runs south to warehouses on the northeastern edge of the runway extension.
(7) Includes the area west of the road from the point where Zeus Boulevard turns sharply north to become Olympus Drive to the point where a wide dirt road runs northeast.
(8) Includes the eastern portion of the grassy area north of the wide dirt road and northwest of Olympus Drive to the point where this drive joins with Lagoon Road.
(9) Both sides of the road from the end of the previous area to the point where a dirt road turns north to the Coral Sands beach pavillion.
(10) Both sides of the road from the Coral Sands turnoff to the entrance to the helipad but excluding areas in footnotes 11 and 13 below.
(11) The area north of the road and outside the Zar Transmitter shielding fence from a point southwest of Camp Hamilton and bounded on the southeast by the road to administrative building 1012.
(12) Grassy area across the road and northwest of the helipad bounded by the road mentioned in 11 and by water storage facilities to the northeast.
(13) Only very limited habitat occurs on both sides of the road in this strongly developed area. All shorebirds seen were in the road or near its edges.

ATOLL RESEARCH BULLETIN

NO. 343

INTERISLAND MOVEMENTS OF FRUIT BATS (*PTEROPUS MARIANNUS*) IN THE MARIANA ISLANDS

BY

G. J. WILES AND P. O. GLASS

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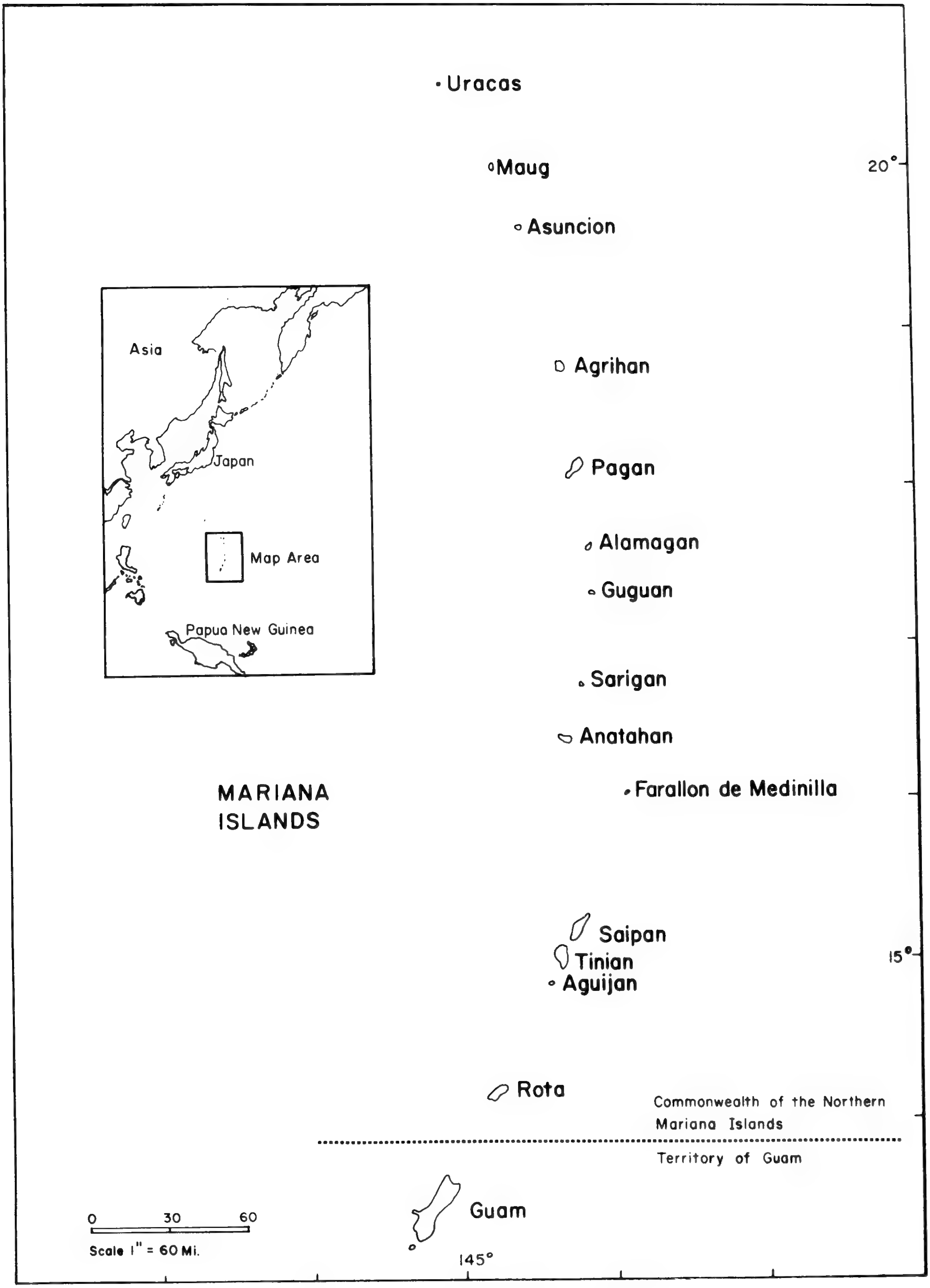

Figure 1. Map of the Mariana Islands.

INTERISLAND MOVEMENTS OF FRUIT BATS (PTEROPUS MARIANNUS) IN THE MARIANA ISLANDS

BY

G. J. WILES[1] AND P. O. GLASS[2]

Fruit bats of the genus Pteropus are considered to be strong fliers (Kingdon, 1974; Nowak and Paradiso, 1983), with some species commuting distances of 10-50 km between day roosts and feeding areas (Breadon, 1932; Ferrar, 1934; Hall, 1983; Lim, 1966; McWilliam, 1985-1986; Ratcliffe, 1932; Taylor, 1934; Walton and Trowbridge, 1983). Longer seasonal movements of $\geq$ 100 km are known for several species of Australian Pteropus, which change roosting sites in response to shifting patterns in the availability of flowers and fruits (Nelson, 1965). However, for most members of the genus, movements remain poorly understood. This is especially true for populations of Pteropus in the Pacific Ocean, many of which are restricted to small islands or small island groups.

Islanders in the Mariana Islands of the western Pacific occasionally report Marianas fruit bats (P. mariannus) flying between islands, but their sightings have never been substantiated by biologists (Perez, 1972; Wiles et al., 1989). Because these fruit bats regularly fly along the shorelines of islands and may fly $\geq$ 1 km out to sea before returning to land, casual observers may mistakenly interpret this behavior as indicative of bats arriving from or departing for a neighboring island. Herein, we document recent evidence of interisland movements of P. mariannus in the southern Marianas based on information collected from 1978 to 1988. Because of recent declines in populations on these islands (Wiles, 1987a; Wiles et al., 1989), it is necessary to understand the extent to which populations on different islands intermingle and whether declines on one island affect population sizes on neighboring islands.

The Mariana Islands are composed of 15 islands extending from 13°14'N, 144°45'E to 20°33'N, 144°54'E, a north-south distance of 750 km (Fig. 1). Descriptions of individual islands appear in Fosberg (1960) and Wiles et al. (1989). Most islands in the southern Marianas are considerably larger (Guam, 540 km^2; Rota, 85 km^2; Aguijan, 7 km^2; Tinian, 102 km^2; and Saipan, 123 km^2) than the 10 northern islands, which range in size from 1-48 km^2. Distances between neighboring southern islands are: Guam to Rota, 60 km; Rota to Aguijan, 78 km; Aguijan to Tinian, 9 km; Tinian to Saipan, 5 km; Saipan to Farallon de Medinilla, 85 km; and Saipan to Anatahan, 119 km. In the northern Marianas, interisland distances range from 29-100 km. All islands have a maximum elevation ranging from 168-965 m with the exception of Farallon de Medinilla, which has a maximum elevation of 81 m. All islands are visible in clear weather from the tops of adjacent islands.

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Pteropus mariannus, a relatively large fruit bat with a forearm length of 135-154 mm, a wingspan of 860-1,085 mm, and a weight of 330-620 g, inhabits all islands from Guam to Maug. Two subspecies of this bat are recognized in the Marianas, with P. m. mariannus inhabiting the islands from Guam to Saipan (Kuroda, 1940) and P. m. paganensis occurring on Pagan and Alamagan (Yamashina, 1932). The precise taxonomic status of P. mariannus on the remaining islands north of Saipan has not been determined. A second smaller species, P. tokudae, is endemic to Guam and is believed to be extinct (Wiles, 1987a).

Much of our data on movements involves large groups of from 50 to several hundred P. mariannus traveling between islands in the southern Marianas. The fruit bats of these islands have been studied in greater detail than those of the northern Marianas, and their population sizes have been estimated about once a year or more often, by use of techniques similar to those described in Wiles (1987a). Numbers of fruit bats on Guam grew from < 50 animals to approximately 850-1,000 bats between 1978 and 1983 (Wheeler and Aguon, 1978; Wiles, 1987a), but have fluctuated between 400 and 800 bats since then. Nearly all bats on Guam live at the northern end of the island in a single colony, which occasionally divides into several smaller aggregations. Since 1984, virtually all young bats on the island have been lost to heavy predation by an introduced species of snake (Boiga irregularis) (Wiles, 1987b). Initial observations of bats on Aguijan, Tinian, and Saipan in 1983 and 1984 revealed populations of < 25-50 bats on each island. Numbers increased to about 75-100 animals on Saipan in 1985 or 1986 and to about 300 animals on Aguijan in 1987 or 1988. Several attempts to census fruit bats on Rota were made between 1979 and 1985 (Wheeler, 1980; Wiles et al., 1989), but we believe that these preliminary surveys underestimated the population there. From 1986 to 1988, more reliable counts were conducted 2-4 times per year and detected a sudden decline in numbers from about 2,500 to 1,300 animals during 1988. Populations of P. mariannus were censused infrequently on only a few of the northern islands since the surveys of Wiles et al. (1989) in 1983 and 1984.

Our conclusion that significant numbers of Marianas fruit bats fly between islands in the southern Marianas on an irregular basis is supported by strong circumstantial evidence and eyewitness accounts. Six examples are based on noticeable and sudden increases in the numbers of bats too large to be explained solely by other factors such as natural recruitment within the resident population on individual islands. In addition, based on information obtained independently from local residents or other biologists, several of these movements closely followed disruptive disturbances at colonies on adjacent islands. Also, several fishermen provided accounts of interisland flights. Two of the fishermen were in boats ≥ 5 km offshore when they saw bats flying overhead.

Known flights of large groups of fruit bats between islands in the southern Marianas since 1978 usually involved bats originating from Rota. Wiles (1987a) reported evidence of two groups of bats flying to Guam from Rota. The first of these probably occurred in early 1979 (wrongly reported as 1980 in Wiles, 1987a), when a colony of about 225-250 bats was discovered on Pati Point, Guam, following a period of several years when the island had no known bat colonies and the entire population was believed to contain < 50 animals (Wheeler and Aguon, 1978). Continued observations of this colony revealed that it temporarily split into two groups located 1.1 km apart in 1981. The estimated combined number of animals at both sites rose from 240 bats in early April 1981 to 508 bats in mid-May 1981. The appearance of the colony in 1979 and its more than doubling in size in 1981 almost certainly resulted from two separate emigrations of bats from Rota, the closest island to Guam and the only island in the southern Marianas with a sizable population of P. marinannus at the time. The movement in 1981 most likely was caused

by human disturbance. Supporting evidence came from a fruit bat hunter interviewed on Rota who, with three other men, killed about 60 bats with shotguns at a roost on the island's southwestern cliffline, and then watched the remainder of the colony, about 150-250 bats, fly south over the ocean toward Guam. The approximate date of the incident coincided within several weeks of the date when the increase in bats was first noted at Pati Point.

A third instance of bats moving between Rota and Guam occurred in 1988, with an abrupt increase in numbers of fruit bats occurring on Pati Point between 26 January and 28 January, when the colony grew from approximately 400 to 709 bats. Before this, Guam's entire population of P. mariannus was estimated at about 500 bats. This change in number occurred about 14 days after Rota was devastated by heavy winds from Typhoon Roy, a severe storm that defoliated most of the island's forest canopy. After the storm, large numbers of bats foraged widely around the island during daylight hours, a highly unusual occurrence. Also, a dramatic increase in illegal hunting occurred during this period. On 26 January, during a study of the effects of the storm on the bat population, biologists inadvertently disturbed a colony on the southwestern side of the island when shifting winds blew their odor to the colony. They observed approximately 250 bats take flight and head over the ocean in the direction of Guam.

In May 1988, the number of fruit bats on Pati Point declined from about 700 to 400 animals. Subsequent ground searches and an aerial survey of northern Guam detected no other colonies. Presumably, the missing bats had departed for Rota, but counts made there in July and November 1988 were not sufficiently reliable to substantiate this. One or more similar movements may have occurred in 1973 or 1974, and are a potential explanation for the apparent absence of colonies on Guam between 1974 and 1979 (Wheeler and Aguon, 1978; Wiles, 1987a).

In July 1985, a small colony of about 50 P. mariannus appeared on Aguijan (D. T. Aldan, pers. comm.), where previously a population of < 10 fruit bats was present (Wiles et al., 1989). The bats probably emigrated from Rota, rather than the nearby islands of Tinian or Saipan. This increase in numbers was first noticed about a week after a poaching incident at a colony at Uzulon Hulo on Rota's north coast. Subsequent annual counts of bats on Aguijan indicated that bat numbers remained fairly steady through 1987. A second larger increase in the island's bat population was reported by visiting goat hunters in March 1988, and was substantiated 3 months later in a survey in which about 300 bats were estimated to be on the island. This movement possibly was caused by the extensive hunting on Rota that continued for several months after Typhoon Roy.

Between 1985 and 1986, the fruit bat population on Saipan increased from < 50 bats to about 75-100 bats. This growth was probably related to immigration and limited natural recruitment. There are two reliable reports from fishermen of small numbers of fruit bats flying to Saipan in May and July 1985. Both men were fishing on the island's northernmost coast and saw bats flying directly in from the north. One man saw a single group of three bats whereas the other observed several groups of two or three bats each in an hour-long period at dusk. The bats probably came from Anatahan, which has the largest population of P. mariannus in the Marianas (Wiles et al., 1989). Farallon de Medinilla, the next island north of Saipan, is small (0.9 km^2), has almost no suitable habitat for fruit bats, and is not known to support bats.

Other sightings have been made of P. mariannus flying singly or in small groups between islands in early evening or at night. Wiles et al. (1989) twice observed individual

bats 3 km south of Guguan at dusk flying toward Sarigan, 63 km distant. A fisherman, who was 5 km south of Rota, saw several small groups of bats flying at night toward Guam on two occasions in the early 1980s. Several decades ago, another fisherman saw a single bat fly over his boat at sea between Alamagan and Pagan, which are 41 km apart.

Movements of P. mariannus between islands may be prompted by overpopulation, dispersal of young, or seasonal variations in food supplies, particularly on small islands with a low diversity of food plants. Typhoons may also cause temporary reductions in the abundance of fruits and flowers eaten by fruit bats, possibly resulting in the emigration of bats to other islands. It is unknown whether bats on certain islands in the Marianas ever commuted daily to feed on nearby neighboring islands, e.g. between Saipan and Tinian, or Tinian and Aguijan. There is no evidence of a seasonal periodicity in the movements of P. mariannus, such as reported for other species of fruit bats in Australia and Africa (Nelson, 1965; Thomas, 1983).

Interisland movements probably occurred more frequently in former times when bat populations were larger. At present, populations of P. mariannus in the southern Marianas are extremely small with densities ranging from about 0.2 to 29.4 bats per km^2 (Wiles et al., 1989). Because of their reduced numbers, the relatively few remaining fruit bats presumably have abundant food resources and probably face seasonal food scarcities only on rare occasions. Under these conditions, animals may have little need to disperse to other islands. In contrast, fruit bats may travel more frequently among the northern Mariana Islands where bat populations are considerably larger.

Hunting and other forms of human disturbance at roosts were probably responsible for at least four of the six movements of large groups described herein. Illegal hunting is a serious problem in the southern Mariana Islands (Wiles et al., 1989), with major bat roosts visited by hunters one to several times per year on Rota and Guam. P. mariannus is sensitive to human odor and easily frightened while roosting, perhaps because the species has been hunted for centuries by islanders. Colonies are particularly vulnerable to disruption by people and normally react by relocating to another site on the same island, although occasional flights to other islands can result.

In the instances reported herein, fruit bats had a tendency to emigrate to islands that were directly visible from their colonial roosts. Examples of this included flights by two groups of bats from roosts in southern Rota to Guam, and another group in northern Rota that departed northward to Aguijan.

Rota is one of several key islands in the Marianas where efforts to conserve fruit bats are essential. The island has the only viable population of P. mariannus in the southern Marianas and is a major source of dispersing bats, which can recolonize neighboring islands. It is necessary that Rota's bats receive adequate protection from overhunting and that a population of 2,500 or more animals be maintained on the island.

In light of the interisland movements described herein, wildlife managers should consider all fruit bats in the southern Marianas as belonging to one contiguous population. P. mariannus currently is protected by local legislation throughout the island chain, but only the population on Guam is officially listed as endangered by the U. S. Fish and Wildlife Service. Populations on Aguijan, Tinian, and Saipan are candidate endangered species (category 1) and are scheduled for listing at an undetermined future date by the U.S. Fish and Wildlife Service. Fruit bats on Rota are a category 2 candidate endangered

species, a designation that requires additional information on status before listing can occur.

The presence of two subspecies of P. mariannus in the Mariana Islands indicates that two separate bat populations occur in the island chain. These populations, if truly distinct, would be separated by a single large expanse of water acting as a barrier to movement between two islands. Such a barrier would have to occur somewhere between Saipan and Alamagan, the distributional limits thus far determined for the two subspecies. However, no exceptionally large distances occur between these islands. Excluding the small and somewhat out-of-the-way island of Farallon de Medinilla, the greatest separation between any two islands in this portion of the archipelago occurs between Saipan and Anatahan. As previously noted, there is good evidence that fruit bats fly between these two islands. The recognition of two subspecies of P. mariannus in the island chain may be incorrect, based on the hypothesis that bats are able to move between all islands, thereby facilitating gene flow throughout the archipelago. A reevaluation of the taxonomic status of P. m. paganensis should be conducted with a much larger sample of specimens, and may reveal this subspecies to be synonymous with P. m. mariannus. Yamashina's (1932) description of P. m. paganensis was determined from a sample of four animals.

To date, there have been no efforts to tag or mark P. mariannus in the Mariana Islands. Such studies would provide better information on the extent and frequency of movements between islands. If tagging is conducted to examine localized movements, investigators should monitor bat populations on neighboring islands for the presence of marked animals.

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ATOLL RESEARCH BULLETIN

NO. 344

THE CORAL REEFS OF GOLFO DULCE, COSTA RICA: DISTRIBUTION AND COMMUNITY STRUCTURE

BY

JORGE CORTÉS

ISSUED BY

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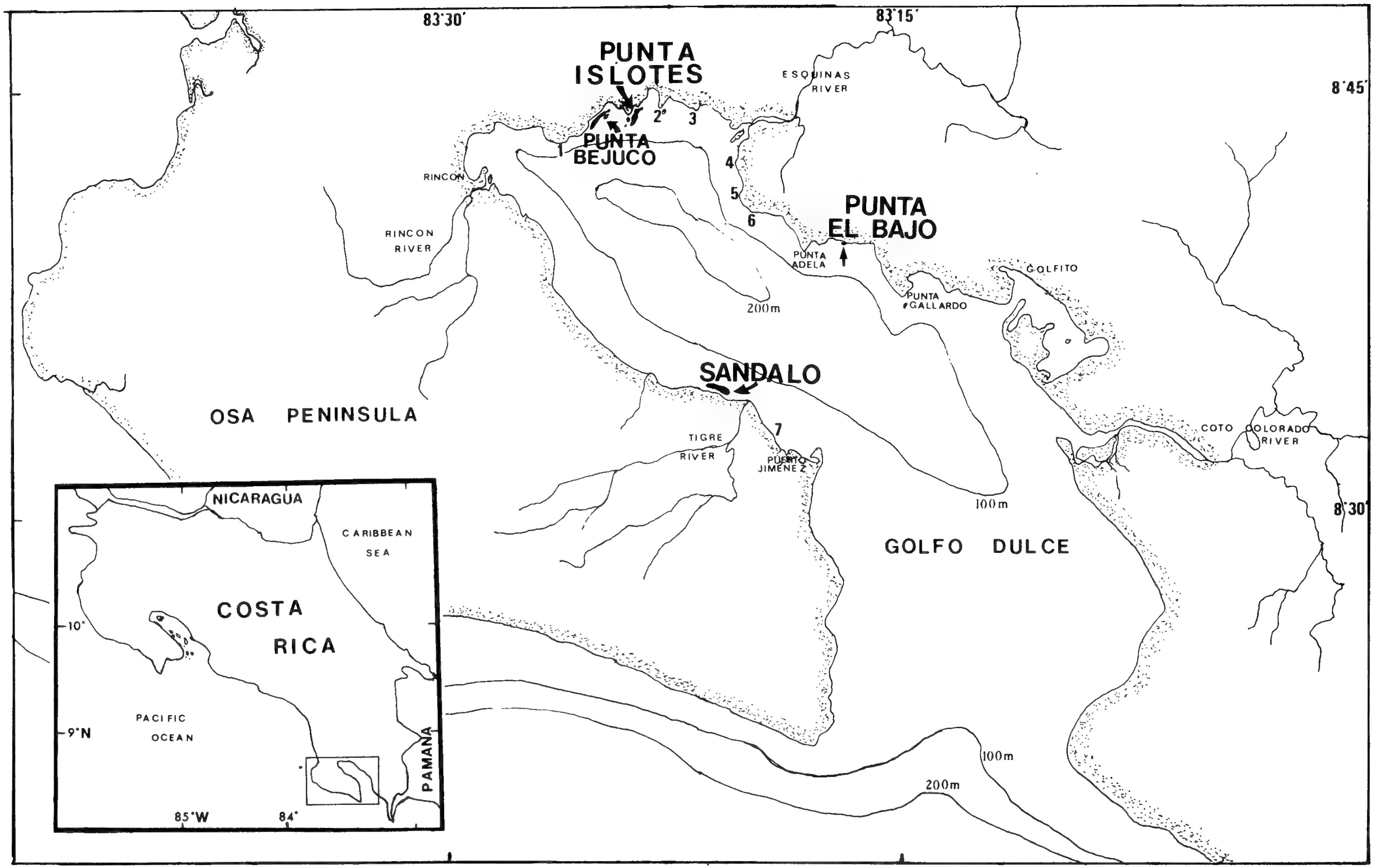

83°30'
83°15'
8°45'
8°30'
PUNTA ISLOTES
PUNTA BEJUCO
ESQUINAS RIVER
RINCON
RINCON RIVER
PUNTA EL BAJO
PUNTA ADELA
PUNTA GALLARDO
GOLFITO
1
2
3
4
5
6
7
200m
SANDALO
OSA PENINSULA
TIGRE RIVER
PUERTO JIMENEZ
COTO COLORADO RIVER
100m
GOLFO DULCE
200m
NICARAGUA
CARIBBEAN SEA
COSTA RICA
PACIFIC OCEAN
PAMANA
10°
9°N
85°W
84°

THE CORAL REEFS OF GOLFO DULCE, COSTA RICA: DISTRIBUTION AND COMMUNITY STRUCTURE

BY

JORGE CORTÉS

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$\Longleftarrow$

Figure 1: Map of Golfo Dulce with indication of the reef areas. Dead reefs observed at: 1- Punta Estrella, 2- Mogos, 3- Playitas (aerial photograph, Fig. 16), 4- Punta Saladero (aerial photograph, Fig. 13), 5-Punta Esquinas, 6- Punta Cativo, 7- dead reef west of Puerto Jiménez. Map based on sheet CR2CM-9 (Golfito), scale 1:200,000, Instituto Geográfico Nacional, San José, Costa Rica.

Manuscript received 6 February 1990; revised 3 July 1990

1 ABSTRACT

The fringing coral reefs of Golfo Dulce, Pacific coast of southern Costa Rica, can be divided into two types. (1) Inner Gulf reefs (Punta Islotes and Punta Bejuco) characterized by high coral coverage of live and dead *Porites lobata* on the periphery and dead *Pocillopora damicornis* and *Psammocora stellata* at the center, low coral diversity, and high topographic relief with a steep front and sides. These reefs are located on the north shore of the Gulf. (2) Outer Gulf reefs (Sándalo and Punta El Bajo), characterized by a relatively high live coral coverage, high species diversity and low relief. At Sándalo, a low profile *Pocillopora-Porites* reef is located on the south shore of Golfo Dulce, *Porites lobata* predominates on the shore-side with *Pocillopora damicornis* and three other species of corals covering most of the seaward side. The reef at Punta El Bajo is a low profile *Psammocora* reef located on the north shore of the Gulf, east of the Punta Islotes reef. This *Psammocora* reef is characterized by a central area approximately $50m^2$ consisting of 100% live *Psammocora stellata* with live *Porites lobata* on the periphery. The community structure of the inner reefs of Golfo Dulce contrasts with other predominantly *Pocillopora* coral communities described from the eastern Pacific in that *Porites lobata* predominates at the reef-edge and slope and surrounds a *Pocillopora-Psammocora* reef-flat. The Punta El Bajo reef is also unique because no reef with 100% live *Psammocora* coverage has been described elsewhere in the eastern Pacific.

The difference between the inner and outer Gulf reefs may be related to two factors. (1) Tectonics – the north side of Golfo Dulce, where the inner Gulf reefs are located, is subsiding, which would explain their thicker accumulations. In contrast, the Sándalo and Punta El Bajo areas are not subsiding; in fact, they may be uplifting. (2) Siltation – the Sándalo and Punta El Bajo reefs are exposed to less terrigenous sediments than the inner Gulf reefs, which may explain the difference in live coral coverage and coral diversity.

Environmental conditions at Golfo Dulce were conducive to reef growth in the recent past but are now deteriorating. Siltation seems to be the main cause of coral reef demise at Golfo Dulce. Coastal areas around the inner Gulf reefs have been totally cleared of forest, exposing the red latosol soil to erosion. Deforestation, combined with poor agricultural practices, mining and the construction of roads have increased the sediment loads on the reefs, especially on the north shore.

2 INTRODUCTION

Coral reef development in the eastern Pacific was once considered meager to non-existant (e.g., Stoddart, 1969), but it has now been demonstrated that there are many reefs and coral communities in the area (for a summary see Glynn and Wellington, 1983). It has also been shown that some of these reefs have high accretion rates – 7.5m/1000yr (Glynn and Macintyre, 1977). The reefs in Costa Rica are found only in the southern part of the country (Glynn et al., 1983; Cortés and Murillo, 1985; Guzmán and Cortés, 1989a). Coral reef development on the northern Pacific coast of Costa Rica is restricted by upwelling (Glynn et al., 1983), but not on the southern nonupwelling section of the coast (Cortés and Murillo, 1985), including Isla del Caño (Guzmán, 1986; Guzmán and Cortés, 1989a) and Golfo Dulce.

Golfo Dulce is an enclosed embayment of tectonic origin located on the southern Pacific coast of Costa Rica (Fig. 1). It is located in one of the wettest regions of the country (Coen, 1983) and there are four major rivers flowing into it, two in the inner part and two near the Gulf mouth. These conditions would not appear to be conducive to coral reef development and the area was ignored by reef workers (e.g., Durham and Barnard, 1952) until the mid-1970's when almost by chance P. W. Glynn (pers. comm., 1985) overflew the Gulf and discovered extensive reef development. In 1978, he surveyed Golfo Dulce and found many coral reefs on the north and south shores of the Gulf, which he later described together with other reefs and coral communities of Costa Rica (Glynn et al., 1983). In order

to assess the impact of the 1982-1983 El Niño disturbance, Golfo Dulce was surveyed again by Glynn and collaborators during February 1985. At that time it became apparent that (1) the reefs in the inner Gulf were different from the reefs of the outer Gulf, and (2) that the reefs in Golfo Dulce were in a state of decline possibly because of terrigenous sediments.

This paper describes and contrast the distribution of reefs and coral communities in Golfo Dulce in reference to their community structure and the associated sediments. Emphasis is given to a large coral reef (Punta Islotes) off the inner north Gulf shore (Fig. 1).

3 DESCRIPTION OF GOLFO DULCE

Golfo Dulce is located between $8^{0}27'$ and $8^{0}45'$N and $83^{0}07'$ and $83^{0}30'$W in the southern Pacific coast of Costa Rica (Fig. 1). It is oriented from NW to SE, is about 50km long and 10 to 15km wide, and covers an area of approximately $680km^2$. The inner part of Golfo Dulce has a maximum depth of slightly over 200m and there is a 60m deep sill at the opening to the Pacific Ocean (Fig. 1). It is similar to high latitude fjords both in bathymetry and the presence of anoxic deep waters (Richards et al., 1971).

3.1 GEOLOGY AND SOILS

The southern sector of Costa Rica is tectonically very active and it is uplifting (Morales, 1985; Obando, 1986; Gardner et al., 1987; Wells et al., 1988), however, Golfo Dulce is considered to be a modern pull-apart basin, where subsidence is active (Fischer, 1980; J. A. Obando, pers. comm., 1985; Berrangé, 1987a; Berrangé and Thorpe, 1988). Geologically, the western and northern sides of Golfo Dulce, known as the Fila Golfito, are formed by the Golfito Terrane, which is deeply weathered and covered by a thick, reddish-brown latosol (Obando, 1986; Baumgartner et al., 1989). The far eastern side of the Gulf consists of low lands of Quaternary alluvial origin, dominated by the Coto-Colorado River and the northern section of the Burica Peninsula, which is made up mainly of the Burica Terrane (Baumgartner et al., 1989). On the southern side, Golfo Dulce is bounded by the Osa Peninsula consisting of ophiolitic lavas of the Nicoya Complex (Santonian to Middle Eocene), the Osa Group conglomerates (Late Pliocene), and the Puerto Jimenez Group (Late Pliocene to Holocene), which contains alluvial sediments (Berrangé, 1987b; Berrangé and Thorpe, 1988).

3.2 RAINFALL AND TEMPERATURES

The Golfo Dulce area receives 4,000–5,000mm of rain per year (Coen, 1983; Herrera, 1985). Data from two stations within the Gulf area, Playa Blanca ($8^{0}40'$N; $83^{0}25'$W) and Esquinas ($8^{0}44'$N; $83^{0}20'$W) and from two nearby stations, Palmar Sur ($8^{0}57'$N; $83^{0}28'$W) and Coto 47 ($8^{0}36'$N; $82^{0}59'$W), indicate that it rains every month of the year, with an average annual peak of 800mm in October. The driest months are December through March, with 100mm or less per month, except at Esquinas where the minimum was 160mm (Herrera, 1985; I.M.N., 1989). The air temperature at Palmar Sur in 1988 was 26.1 ± 0.78^{0}C (mean and standard deviation), and at Coto 47, 26.8 ± 0.57^{0}C, with a range of 18 to 35^{0}C, for both stations (I.M.N., 1988). Average hours of sunlight per day at Palmar Sur ranges from 3.4 to 10.4 (I.M.N., 1988). The lowest values occur between August and November, while the

higher values occur between December and March. This corresponds with the wet and dry seasons, respectively, as noted above.

3.3 VEGETATION

The vegetation around the Golfo Dulce area corresponds to the Tropical Wet Forest type in the Holdridge Life Zone System (Allen, 1956; Holdridge et al., 1971). It is the only area with this type of forest still extant on the Pacific side of Central America (Hartshorn, 1983). Mangrove forests of different types and sizes are found around the Gulf. The most extensive are found at the mouths of the largest rivers, Coto-Colorado, Esquinas and Rincón (Allen, 1956; Jiménez and Soto, 1985). Since 1983 there has been a considerable increase in deforestation that corresponds with the opening of a road connecting the Osa Peninsula with the Interamerican Highway. In the past 50 years road construction in different parts of Costa Rica has resulted in extensive deforestation (Sader and Joyce, 1988).

3.4 TIDES AND CIRCULATION

Golfito (8^{0}39'N; 83^{0}11'W) is the only locality in the Golfo Dulce area where tidal data are available. It is a subordinate station to the reference station at Puntarenas, Costa Rica (9^{0}58'N; 84^{0}50'W). Tidal differences and other constants for Golfito, as well as tidal predictions for Puntarenas, can be found in the National Ocean Service Tide Tables (U.S. Department of Commerce, 1988). The tides are semidiurnal, with a mean range of 2.35m and a spring range of 2.89m (U. S. Department of Commerce, 1988). In this paper all depths cited are referenced to mean low water (MLW).

The currents of Golfo Dulce have not been studied, but field observations (*in situ*, from aerial photographs and river delta morphology) indicate that water circulation is similar during both ebbing and flooding tides. Apparently there is a counter-clockwise flow of water into the Gulf along the eastern and northern shores and out along the western and southern shores (Fig. 2). During the dry season (December to May), there are strong southeasterly winds during the afternoons that create a moderate chop in the inner part of the Gulf (pers. obs.).

4 PREVIOUS WORK

Oceanographic data for Golfo Dulce were collected during cruises by the University of Washington's R/V Thomas G. Thompson (Richards et al., 1971; Kuntz et al., 1975). Richards and colleagues visited the Golfo on two brief occasions (1-2 and 10 March, 1969) during cruise #35 of the R/V T. G. Thompson. Five stations were occupied during each of the two visits: one just outside Golfo Dulce, one on the sill and three inside the gulf. They measured salinity, temperature, dissolved oxygen, ammonium, nitrate, nitrite, phosphate, silicate, hydrogen sulfide, alkalinity and pH. The deep inner waters of the Gulf are anoxic and the data taken eight days apart indicated an influx of oceanic water into the basin. Salinity of the surface waters of the inner part of Golfo Dulce ranged from 30 to 32ppt, and the surface temperature between 28 and 31^{0}C. This contrasts with the deep anoxic waters that had salinities around 35ppt and temperatures around 16^{0}C. Similar values to cruise #35 were obtained during cruise #76 of the R/V T. G. Thompson in late January and early February, 1973 (Kuntz et al., 1975). Dr. James J. Anderson (University of Washington) provided another set of oceanographic data from Golfo Dulce, taken during cruise #46 of

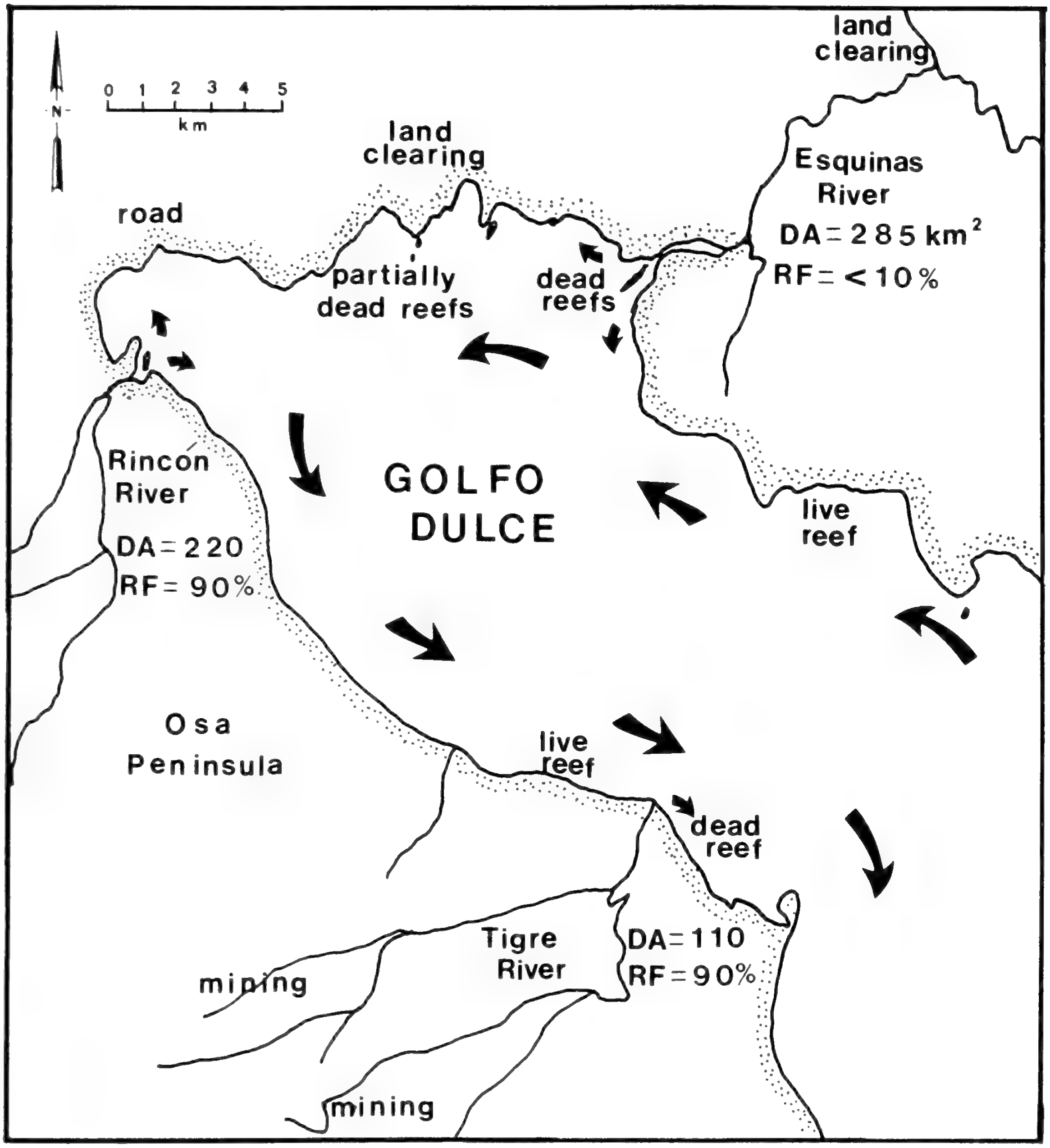

Figure 2: Putative water circulation at Golfo Dulce (large arrows). Direction of sediment movement indicated by small arrows. The main anthropogenic disturbances are indicated. D.A. = drainage area of the three main rivers in km^2. R.F. = remaining forest as of 1988 (D.G.F., 1989). Road refers to the area most affected by road construction.

the R/V T. G. Thompson in January, 1970. These data also indicate very low to no oxygen below 150m with an increase of hydrogen sulphide towards the bottom. The temperatures and salinities recorded during this cruise were similar to those reported previously.

Another paper, published by Nichols-Driscoll (1976), describes the deep, benthic, invertebrate communities of Golfo Dulce from samples collected during cruise #76 of the R/V T. G. Thompson. She found that the abundance and biomass of invertebrates were less than expected for a tropical environment. In addition, she reported that the deeper parts of the Gulf had very few species with low numbers of individuals.

Three main reef areas have been described in Golfo Dulce, two off the northern shore and the other off the southern shore. Most of the reefs in Golfo Dulce are paucispecific, dominated by *Porites lobata* Dana (Glynn et al., 1983). The largest reef off the northern shore at Punta Islotes covers several hectares, and has a well-developed reef-flat (0.5m deep, MLW) composed, for the most part, of dead *Pocillopora damicornis* Linnaeus, and small dead or live hemispherical colonies or large microatolls of *Porites lobata*. The edges, slope and base of these reefs are composed totally of large, live, partly dead or dead massive colonies of *Porites lobata*, with a few isolated colonies of *Pavona gigantea* Verrill and *Psammocora stellata* (Verrill). The reef slope is very steep, 45^0 or more, vertical in some places and extending to 10–13m depth (Glynn et al., 1983; Cortés and Murillo, 1985). Glynn and colleagues suggested that this *Porites* reef on the northern shore could have formed in 3,000–10,000 years (Glynn et al., 1983).

5 METHODS

5.1 CORAL COMMUNITY

The belt-quadrat method was used to quantitatively sample the Golfo Dulce reefs (Weinberg, 1981; Dodge et al., 1982). Areas around the reefs were chosen haphazardly and 10m long transects were sampled along the depth contours. A one square meter quadrat, divided into 100 cells of 10 x 10cm, was moved at each side of a 10m long chain (for a total of $20m^2$ per transect) and the area covered by live coral, dead coral and other substrate (rubble and/or sand) was recorded. Four reefs were studied in some detail: two inner Gulf reefs on the north shore (Punta Islotes and Punta Bejuco), and two outer Gulf reefs, a *Psammocora* reef (Punta El Bajo) also on the north shore, but east of the inner Gulf reefs, and a mixed *Pocillopora-Porites* reef (Sándalo) on the south shore (Fig. 1). Twenty two transects were sampled at the Punta Islotes reef and ten transects at Punta Bejuco in three reef zones: reef-flat (0–1m deep), reef-edge (1–2m) and reef-slope (>2m). At the other reef sites, transects were established along lines across the reefs. Five transects were sampled at Punta El Bajo in two zones: the periphery (shallow and deep) and the central *Psammocora* core. At Sándalo, ten transects were sampled in two zones: inshore (<3m depth) and offshore (>3m).

The percent data from the transect sampling were arcsine-transformed for one-way ANOVA analysis to test for differences between reef zones and inter-reef differences. To determine which mean differences were significant, the Student-Newman-Keuls (SNK) test was employed (Sokal and Rohlf, 1969). Species diversity of corals was calculated using the following indices: Shannon-Wiener (H') and species evenness (J'). Hutcheson's t-test was used to compare the Shannon-Wiener diversity indices (Poole, 1974).

Field observations were conducted mainly in February, 1985 (inner section of the Gulf: north shore east to Punta Islotes; south shore east to Puerto Jiménez) and June-October,

1988 (all of Gulf), and occasionally during other visits to the area in 1987 and 1989.

Depth profiles of the inner Gulf reefs were obtained using a portable echosounder (Raytheon DC 200 Z) during high tide. Depth profiles of the *Pocillopora-Porites* reef (Sándalo) and the *Psammocora* reef (Punta El Bajo) were constructed using measuring tape, compass and depth gauges while SCUBA diving.

5.2 SEDIMENTS

Sediment samples, two replicates per site, were collected from six different zones at the Punta Islotes reef: (a) shore, (b) beach, (c) back-reef, (d) reef-flat, (e) reef-edge and (f) reef-slope. Samples were also collected along transects across other reefs (Punta Bejuco, Sándalo and Playitas, location 3 in Fig. 1). The general appearance and consistency were recorded in the field. The sediment constituents were determined by visual inspection and the carbonate components identified. To determine the percentage of calcium carbonate, a titration method was used, similar to that described by Siesser and Rogers (1971) with modifications by J. Acuña (CIMAR, Universidad de Costa Rica). Size analyses were accomplished by standard sieve techniques with the following sieve sizes: 63, 125, 250, 500, 710, 1000, 2000 μm, USA Standard Testing Sieve (Folk, 1974; McManus, 1988). Size analyses and percent calcium carbonate were determined in triplicate for each sample.

5.3 ANTHROPOGENIC DISTURBANCES

The main human impacts on the Golfo Dulce watershed were determined from field observations, from interviews with people that live or have worked in the area and from the literature. The drainage area of the three main rivers flowing into Golfo Dulce was calculated using a Keuffel and Esser 620015 polar planimeter and 1:50,000 scale maps. The percentage of standing primary forest in the Golfo Dulce area was obtained from aerial photographs with subsequent ground confirmation. Maps depicting the forested areas in 1940 and later are available in Hartshorn et al. (1982), D.G.F. (1983) and Sader and Joyce (1988). The most recent survey was conducted in 1988 and this information is still in preliminary form (D.F.G., 1989), but was used in the present study because these results were confirmed by field observations.

6 RESULTS

6.1 CORAL COMMUNITY

6.1.1 REEF DESCRIPTIONS –

PUNTA ISLOTES:

The coral reef at Punta Islotes (Figs. 3 and 4) can be divided into five zones: back-reef, reef-flat, reef-edge, reef-slope and fore-reef talus. Back-reef: 0–1m deep, is the area between the shore and the reef framework. It is covered by mud and sand. Reef-flat: 0–1m, consists of dead *Pocillopora damicornis* in growth position in some areas (Fig. 5) and as rubble with dead *Psammocora stellata* in others. Also, live and dead microatolls of *Porites lobata* are scattered over the reef flat. The reef-edge: 1–2m depth, marks the transition between the shallow, almost horizontal flat, and the deep and steep slope. The predominant coral species of the reef-edge and slope is *Porites lobata* (Fig. 6). The reef-front descends to a depth of 10–12m to a sand and mud bottom, i.e., the fore-reef talus (Figs. 7 and 8a).

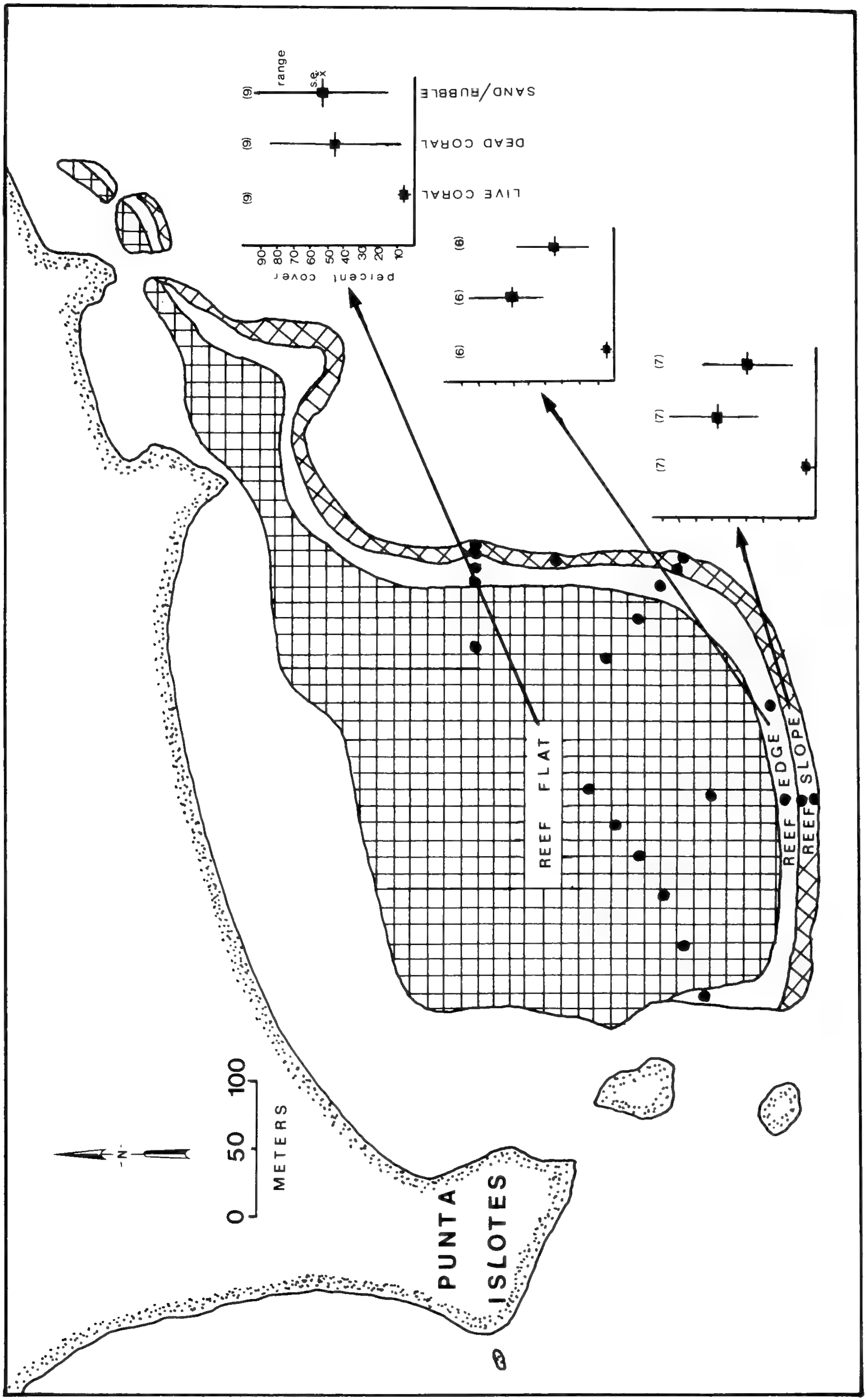
PUNTA
ISLOTES
0
50
100
METERS
N
REEF FLAT
REEF EDGE
REEF SLOPE
LIVE CORAL
DEAD CORAL
SAND/RUBBLE
percent cover
90
80
70
60
50
40
30
20
10
range
s.e.
(9)
(6)
(7)

Table 1: Relative abundances of live corals observed at the four study reefs and elsewhere in Golfo Dulce (see Fig. 1 for locations). Symbols: a = abundant; f = few; r = rare or unique; - = not observed. Species as in Wells (1983)

	LOCALITY					
SPECIES	Punta Islotes	Punta Bejuco	Punta El Bajo	Sándalo	Punta Adela	Punta Gallardo
Pocillopora eydouxi	-	-	-	r	-	-
Pocillopora damicornis	r	-	-	a	-	-
Pavona varians	r	r	-	a	-	-
Pavona gigantea	r	-	-	-	r	a
Psammocora stellata	r	r	a	a	-	-
Porites lobata	a	a	f	a	a	-
Tubastrea coccinea	-	-	-	-	-	f
Oulangia bradleyi	r	-	-	-	-	-
Astrangia browni	r	-	-	-	-	-

A summary of the transect data from Punta Islotes reef is given in Figure 3. The only live coral encountered in the transects was *Porites lobata*, but other live species were observed at the Punta Islotes reef: *Pavona varians* Verrill, *Pavona gigantea*, *Psammocora stellata*, *Oulangia bradleyi* Verrill and *Astrangia browni* Palmer (Table 1). A few small live colonies of *Pocillopora damicornis* were seen in 1985, but not in following surveys. A comparison of the percent cover of live coral, dead coral and sand/rubble in the three reef zones indicats that these are very similar (Fig. 3); statistical testing shows no significant differences (ANOVA, p>0.05, in all cases).

⇐

Figure 3: Percent live coral (LC, only *Porites lobata*), dead coral (DC) and sand/rubble (S/R) at the three reef zones of the Punta Islotes reef: reef-flat (0–1m), reef-edge (1–2m) and reef-slope (>2m). Noted for each type of substrate are the mean percent, standard error of the mean, range, and number of transects. Dots indicate location of transects.

Figure 4: Oblique aerial photograph of the Punta Islotes reef during an extreme low tide, –0.3m (9.III.1989). Reef photographed at approximately 300m elevation.

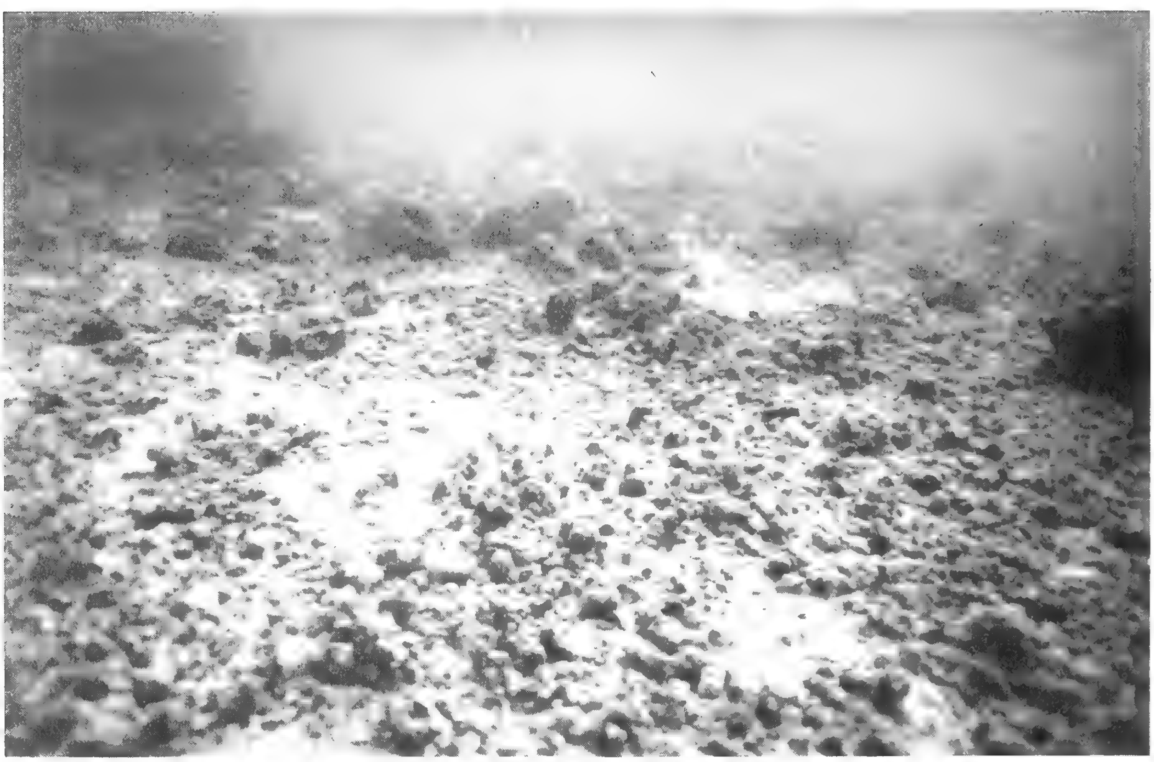

Figure 5: Dead *Pocillopora damicornis* in growth position on the reef-flat of Punta Islotes. Depth 1m. Date: February, 1985. Distance across the middle of the photograph is 1.5m. Photograph by P. W. Glynn.

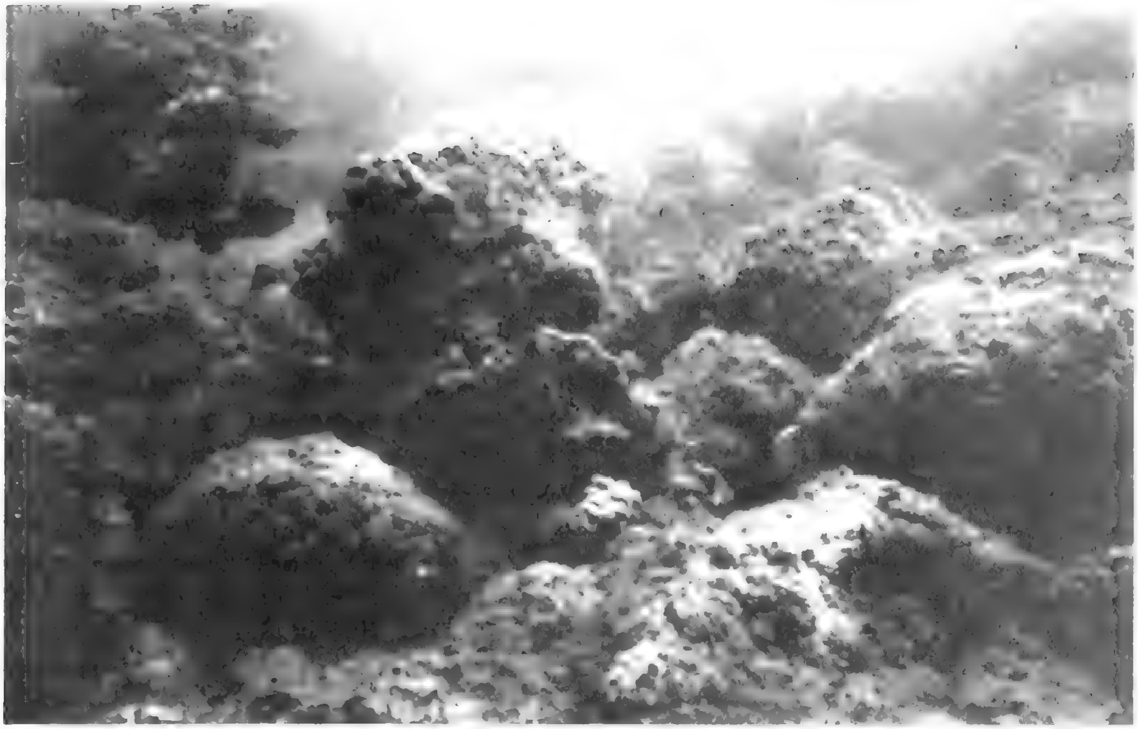

Figure 6: Live knobs of *Porites lobata* over large dead colonies of the same species from the reef-edge of Punta Islotes. Depth 2 m. February, 1989. Distance across the middle of the photograph is approximately 4m. Photograph by I. G. Macintyre.

Figure 7: Base and fore-reef talus of the reef at Punta Islotes. The base is made up by dead colonies of *Porites lobata*. The fore-reef talus sediments consist of sand, mud and fragments of various sizes of *P. lobata*. Depth 10m. February, 1989. Photograph by I. G. Macintyre.

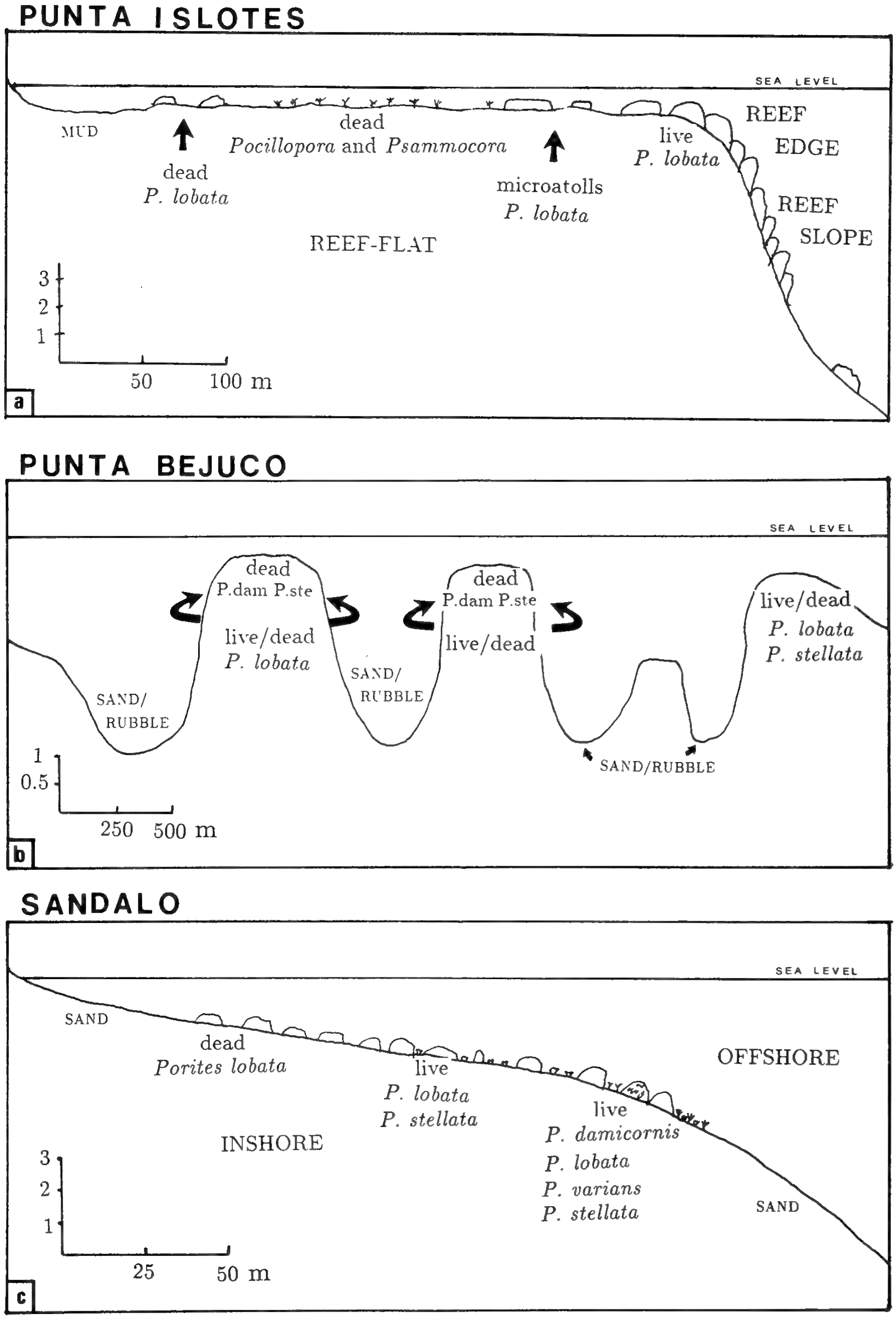

Figure 8: Schematic profiles based on echosound recording and field observations. a. Section perpendicular to shore through the middle of the Punta Islotes reef; b. Section parallel to shore, showing several reefs, Punta Bejuco reef complex. Species: P.dam = *Pocillopora damicornis*, P.ste = *Psammocora stellata*; c. Section perpendicular to the shore at the Sándalo reef.

PUNTA BEJUCO:

The Punta Bejuco reef complex (Fig. 1) includes several reefs separated by sand channels (Fig. 9). The reef fronts and flanks are steep and made up of live and/or dead colonies of *Porites lobata* (Fig. 8b). The central area of the reef consists of dead *Pocillopora* and *Psammocora* rubble. The predominant species in this reef complex is again *Porites lobata* with very low abundances of *Psammocora stellata* and *Pavona varians* (Tables 1 and 2). Live coral cover is low but not significantly different between reef zones. Dead coral cover and sand/rubble cover are high in the three reef zones (Table 2).

PUNTA EL BAJO:

The reef at Punta El Bajo is a small patch reef (Fig. 10) made up of only two species, *Psammocora stellata* and *Porites lobata* (Table 1). The central core of the patch consists of almost 100% live *Psammocora stellata* coverage of the bottom (Table 3). These colonies are tightly interlocked (Fig. 11). A rod was pushed into the *Psammocora* framework at several points, indicating a thickness of at least one meter. Toward the periphery, live *Porites lobata* is present, together with isolated unattached colonies of live *Psammocora stellata*. Live coral cover on the central *Psammocora* core is significantly higher than the shallow and deep periphery (1-way ANOVA, $F = 29.46$, $p<0.05$). Differences between the two zones in terms of dead coral cover and sand/rubble cover are not significant (Table 2-3). Many fragments of dead *Pocillopora damicornis* were observed.

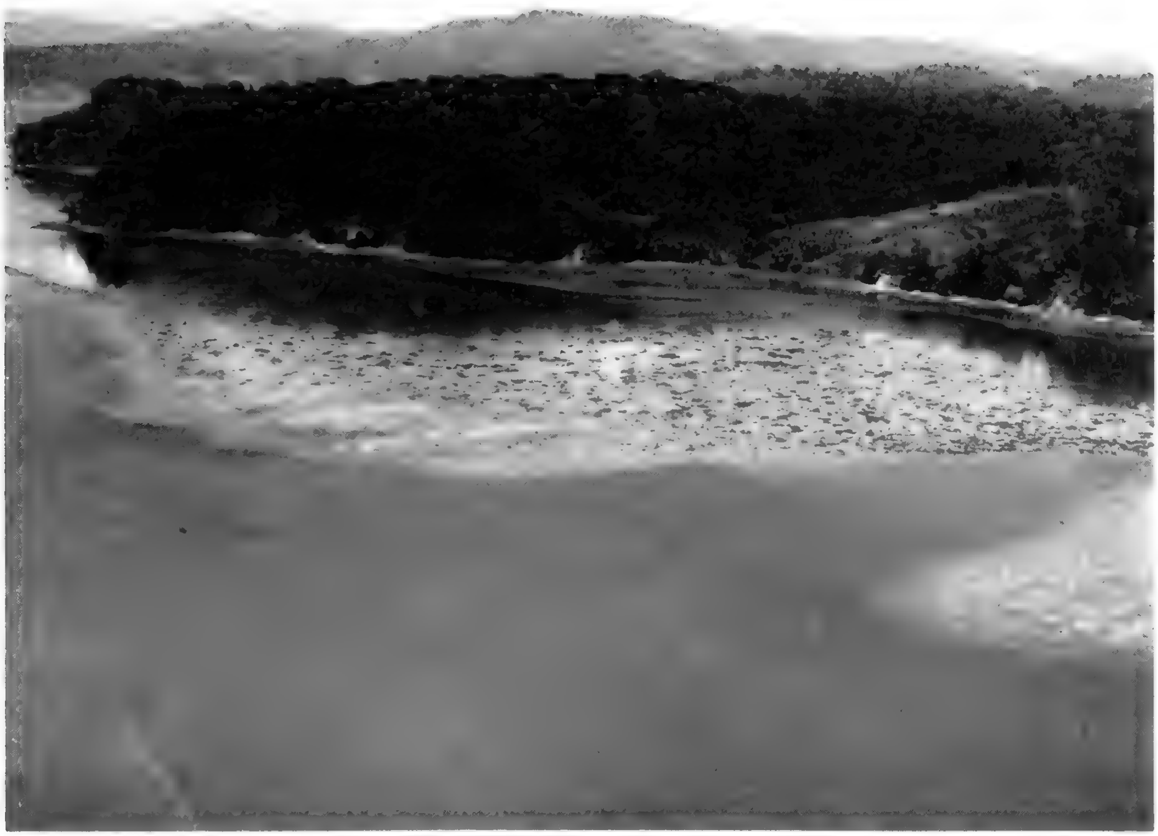

Figure 9: Oblique aerial photograph of the Punta Bejuco reef complex. Note the sediments moving onto the reef from the deforested shore. 9.III.1989. Tidal height -0.2m. Elevation, approximately 250m.

Table 2: Summary of the transect data from the Punta Bejuco reef complex, Golfo Dulce, divided into three reef zones. See Figure 1 for location of reef. The mean percent cover for each zone is given, with the standard error of the mean in parenthesis. Results of ANOVA given below, ns = not significant.

	ZONE		
	Reef-flat	Reef-edge	Reef-slope
depth (m)	0 – 1	1 – 2	2 – 8
number of transects	2	4	4
Pavona varians	0	0	0.1 (0.9)
Psammocora stellata	0	0	0.5 (0.04)
Porites lobata	0.3 (0.1)	0.9 (0.5)	1.2 (0.6)
dead coral (1)	61.1 (2.1)	41.1 (13.8)	55.6 (12.1)
sand/rubble	38.5 (1.9)	58.1 (13.6)	42.9 (11.9)

(1) mainly *Porites lobata* but also *Pocillopora* and *Psammocora* on the reef-flat

ANOVA: live coral $F = 0.34$, $p > 0.25$: ns
dead coral $F = 0.36$, $p > 0.25$: ns
sand/rubble $F = 0.37$. $p > 0.25$: ns

SANDALO:

The reef at Sándalo is over 500 meters long by 100 meters wide; it does not extend into deep water (Fig. 12). The inshore zone consists mainly of dead massive colonies of *Porites lobata*. The coverage by live *Porites lobata* and other species increases seaward (Table 4). Live coral cover is significantly higher offshore than inshore (ANOVA, $F = 14.65$, $p<0.01$). Species diversity also increases seaward, down to a depth of 5 m. Beyond the deepest corals, the sand bottom descends rapidly at a slope of around 20^0 (Fig. 8c). Dead coral cover and the area covered by sand/rubble are not significantly different at the two zones. This is the only reef in Golfo Dulce with a relatively large population of live *Pocillopora damicornis* and other coral species (Table 1). Also, a few live *Pocillopora eydouxi* Milne Edwards and Haime were found on this reef.

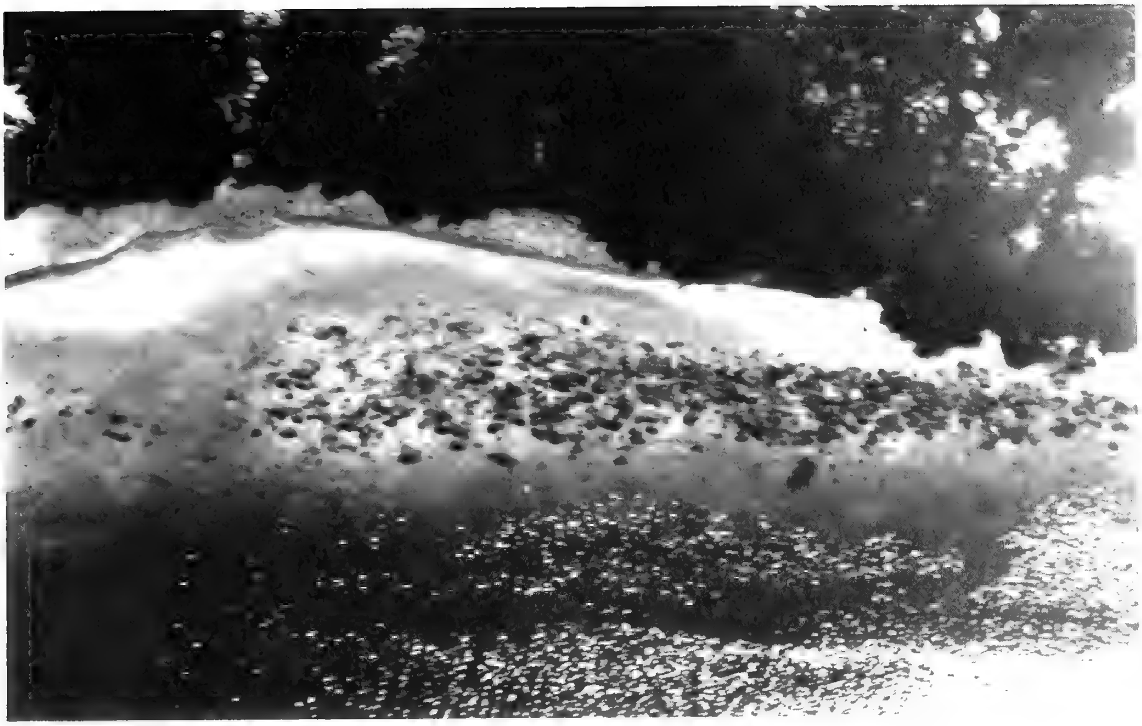

Figure 10: Oblique aerial photograph of the Punta El Bajo reef, 9.III.1989. Tidal height = -0.1m. Altitude = 300m.

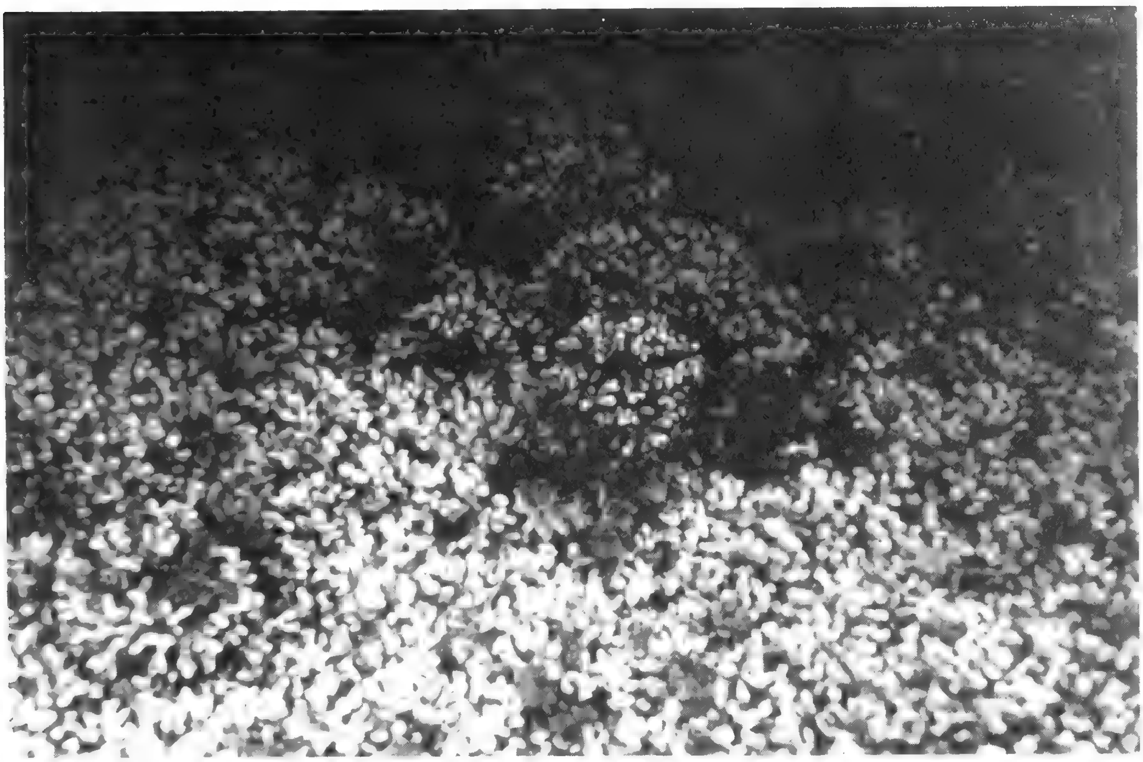

Figure 11: Monospecific stand of *Psammocora stellata* at the Punta El Bajo reef. Depth = 3m. Date = 11.III.1989. Distance across the middle of the photograph is approximately 1 m, branches are about 1cm in diameter.

Table 3: Summary of the transect data from the Punta El Bajo reef, divided into two zones: the periphery (shallow, 3 – 4 m and deep, 7m) and the central *Psammocora* core (5 – 6 m). * = significant at the 5% level, ns = not significant.

	ZONE	
	Periphery	Core
number of transects	3	2
Psammocora stellata	5.6 (3.3)	86.1 (2.2)
Porites lobata	11.6 (5.3)	2.6 (1.1)
dead coral (1)	28.2 (9.7)	10.9 (3.1)
sand/rubble	54.5 (14.9)	0.3 (0.2)

(1) *Porites lobata, Psammocora stellata* and some *Pocillopora damicornis*

ANOVA: live coral $F = 29.46, p < 0.05$ *
dead coral $F = 1.26, p > 0.25$: ns
sand/rubble $F = 9.62, p > 0.05$: ns

Figure 12: Oblique aerial photograph of Sándalo reef, looking seaward, 9.III.1989. Tidal height = –0.3m. Altitude = 200m.

Table 4: Summary of transect data from the Sándalo reef, divided into two zones. Mean percent cover for each zone and standard error of the mean in parenthesis are given. Results of ANOVA given below, ** = significant at the 1% level, ns = not significant.

	ZONE	
	Inshore (2 - 3 m)	Offshore (3 - 5 m)
number of transects	5	5
Pocillopora damicornis	0	8.9 (7.1)
Pavona varians	0	6.8 (5.9)
Psammocora stellata	0.2 (0.1)	0.4 (0.2)
Porites lobata	12.0 (4.5)	29.8 (6.8)
dead coral (1)	64.8 (5.5)	44.8 (5.8)
sand/rubble	23.0 (6.3)	9.2 (3.6)

(1) mainly *Porites lobata* and *Pocillopora damicornis*, some *Psammocora stellata* and *Pavona varians*

ANOVA: live coral $F = 14.65$, $p < 0.01$ **
dead coral $F = 4.98$, $p > 0.05$: ns
sand/rubble $F = 3.48$, $p > 0.05$: ns

OTHER REEF SITES:

Totally dead reefs found at Punta Estrella, Isla Mogos, Playitas, Punta Saladero (Fig. 13), Punta Esquinas and Punta Cativo (for locations see Fig. 1) are made up of *Porites lobata* and some *Pocillopora damicornis* fragments. All of these reefs are located near the Esquinas River, and their surfaces are covered by terrigenous sediments. Colonies of *Porites lobata* are intensely bioeroded mainly by *Lithophaga* spp. and *Gastrochaena rugulosa* Sowerby.

At Punta Adela, there is a small coral community (Fig. 14) with a few live *Porites lobata* colonies, at least one live *Pavona gigantea* colony (Table 1) and many dead colonies of *Porites lobata, Pocillopora damicornis* and *Psammocora stellata.*

At Bajo La Viuda, off Punta Gallardo (Fig. 1) two species of corals, *Tubastrea coccinea* Lesson and *Pavona gigantea* (Table 1), absent or rarely found on other reefs of Golfo Dulce, were abundant. This area consists of a series of submerged rocky outcrops (only one is exposed) with tops at around 2m depth and the bases at 12–15m. These rocky outcrops are covered by a species of the octocoral *Telesto* sp., isolated live colonies of *Tubastrea coccinea* and some large (up to 40cm), live laminar colonies of *Pavona gigantea.* The bottom is composed of sand and rubble.

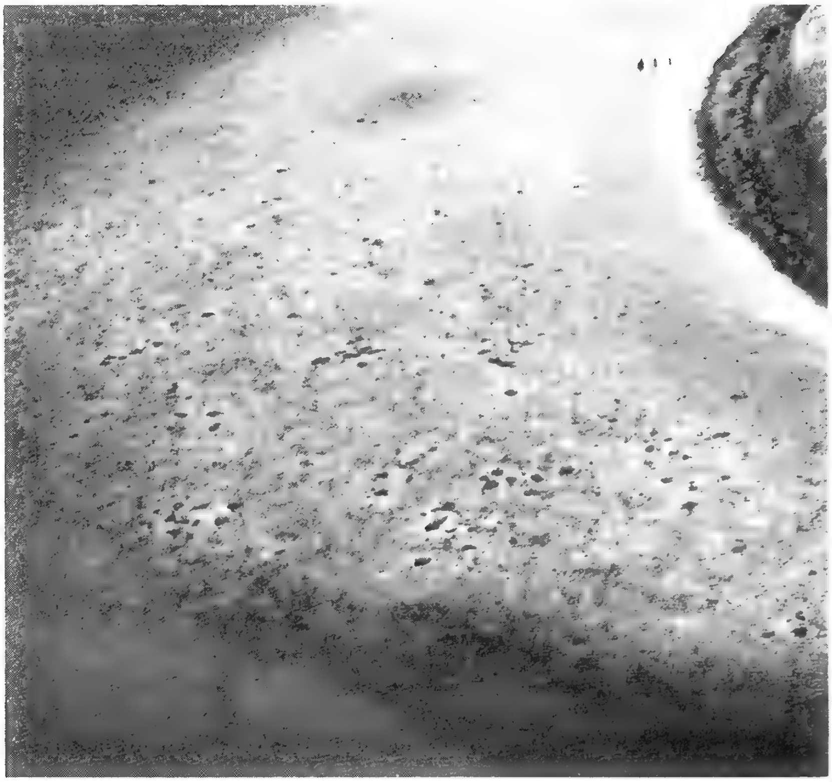

Figure 13: Oblique aerial photograph of the dead reef at Punta Saladero, 9.III.1989. Tidal height = –0.2m. Altitude = 300m.

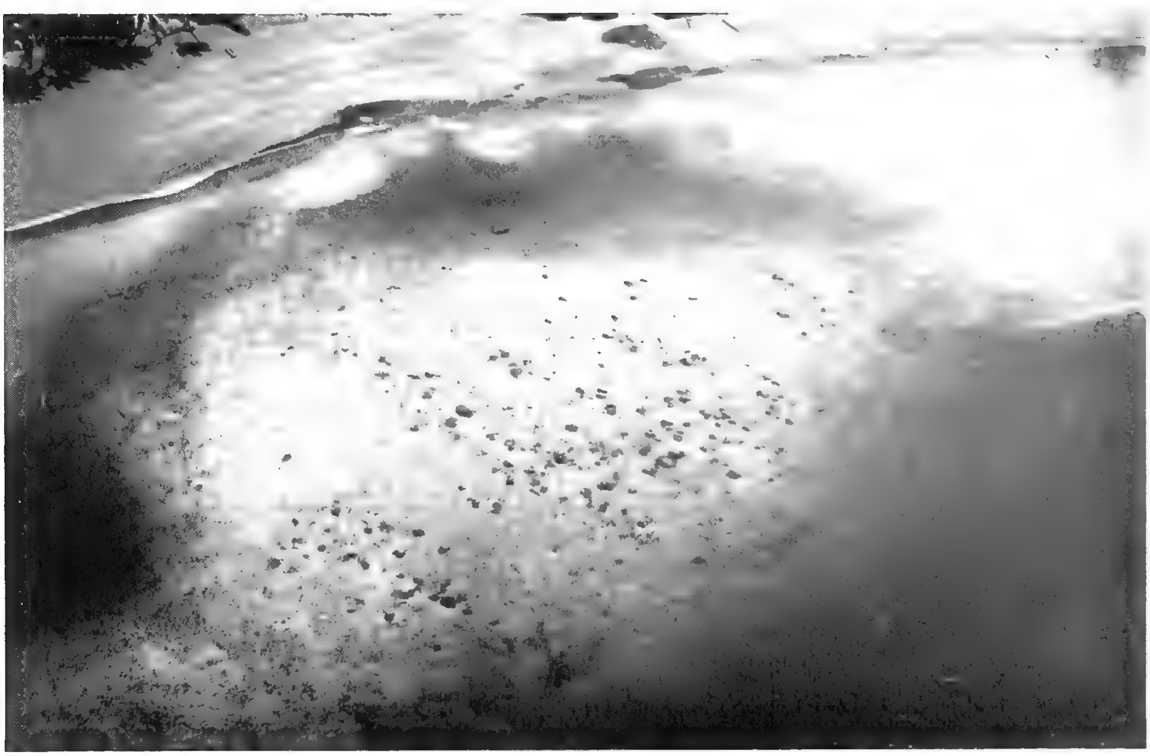

Figure 14: Oblique aerial photograph of the reef at Punta Adela, 9.III.1989. Tidal height = –0.2m. Altitude = 300m.

6.1.2 INTER-REEF COMPARISONS –

Live coral cover is highest at Punta El Bajo, with a mean of 45.9% (Table 5), but with values as high as 93.4% (Table 3), due to the presence of *Psammocora stellata*. The area with the next highest live coral cover is Sándalo with an average of 29.1% (Table 5) and values as high as 49.1% (Table 4). Both at Punta Bejuco and Punta Islotes, live coral cover is low (highest value was 8.4%), while dead coral cover makes up 50% or more of the substrate (Table 5). There were significant differences in live coral cover between reefs (1-way ANOVA, $F = 21.21$, $p<0.05$), dead coral cover ($F = 3.09$, $p<0.05$) and area covered by sand/rubble ($F = 4.00$, $p <0.05$) (Table 6). Results of the SNK test of the above ANOVA (Table 7) indicate that there is no difference between the live coral cover of Punta Islotes and Punta Bejuco, and that they are lower than Sándalo. Live coral cover on Sándalo is lower than and significantly different from Punta El Bajo. In the case of dead coral cover, there is no significant difference between Punta Bejuco, Punta Islotes and Sándalo. At Punta El Bajo, the mean dead coral cover is significantly lower than at the other three reefs because of the high percentage of live *Psammocora stellata*. The area cover by sand/rubble is very similar at Punta El Bajo, Punta Islotes and Punta Bejuco (Table 7). The percentage of sand/rubble at Sándalo is significantly lower than at the other reefs because most of the substrate is covered by live and dead coral.

The inner Gulf reefs on the north side of Golfo Dulce (Punta Islotes and Punta Bejuco) are similar: live and dead *Porites lobata* form the flanks of the reefs and dead *Pocillopora damicornis* in growth position and/or fragments of dead *Pocillopora* and *Psammocora* are found on the reef-flat. Also, most of the reefs have almost vertical fronts and sides, with a topographic relief of up to 12m. The number of abundant coral species (Table 1) and diversity (Table 8) are low. All the diversity indices at Punta Islotes are zero because only one species was encountered (Table 8).

On the south shore of Golfo Dulce, the living reef at Sándalo consists of mostly dead *Porites lobata* in the near-shore, while live *Pocillopora damicornis* and *Porites lobata* are abundant on the seaward side. The highest value of live species diversity of the four reefs studied corresponded to this reef, where evenness was also high (Table 8). The reef at Punta El Bajo has *Porites lobata* on the periphery and live *Psammocora stellata* at the center and exhibits low values of species diversity but high values of species evenness ($J' = 0.669$) because the only two species found were present in similar proportions (Table 8). Coral diversity (Shannon-Wiener index) is significantly higher ($t = 5.749$, $p<0.001$) at Sándalo ($H' = 0.822$), than at Punta El Bajo and Punta Bejuco. Diversity in these last two reefs is not significantly different.

6.2 SEDIMENTS

The sediments from the shore, beach and back-reef of Punta Islotes (Fig. 15a) are mainly brick red and are composed of very fine terrigenous latosol – a soil that has been observed inland in forest clearings and road cuts. The size distribution of the reef-flat sediments was bimodal – consisting of coral (*Pocillopora damicornis* and *Psammocora stellata*) and molluscan fragments with finer sediments including unidentifiable carbonate skeletal fragments, sponge spicules and terrigenous mud. The reef-edge sediments contained a high percentage of fine carbonate material in contrast to the reef-slope sediments that had a high percentage of coarse carbonate grains – mainly molluscs and coralline algae (e.g., *Amphiroa*).

Table 5: Summary of transect data for the four reefs studied. Average percentage coverage of each species, dead coral and sand/rubble are given, with the standard error of the mean in parenthesis.

	REEF			
	Punta Islotes	Punta El Bajo	Punta Bejuco	Sándalo
number of transects	22	5	10	10
Pocillopora damicornis	0	0	0	4.44 (3.82)
Pavona varians	0	0	0.045 (0.004)	3.41 (3.17)
Psammocora stellata	0	37.83 (17.78)	0.025 (0.02)	0.31 (0.01)
Porites lobata	1.71 (0.49)	8.04 (3.78)	0.91 (0.33)	20.92 (4.95)
dead coral	54.34 (5.25)	21.32 (7.06)	50.90 (7.80)	54.79 (5.08)
sand/rubble	43.95 (5.27)	32.81 (14.87)	48.12 (7.71)	16.13 (4.23)

Similarly, the percentage of calcium carbonate in the Sándalo reef sediments increased seaward (Fig. 15b). The coarse sediment fraction consisted mainly of dead coral fragments (*Pocillopora damicornis* and *Psammocora stellata*) and whole and fragmented molluscs. The fine sediment fraction consisted of carbonate silt and sponge spicules.

Samples from two other areas (Table 9) indicated a pattern similar to that described for Punta Islotes with near-shore sediments containing higher percentages of fine terrigenous sediments.

Clay mineral analysis of sediments from north shore reefs revealed two sources of terrigenous input (Cortés and Brass, in prep.). One source is inland with sediment transport to the sea via the Esquinas River. The other source is from nearby hills adjacent to the reefs with sediments supplied by land slides.

Table 6: ANOVA results of the comparisons of mean live coral, dead coral and sand/rubble at the four reefs studied in Golfo Dulce.

LIVE CORAL

LEVEL	SS	DF	MS	Fs
1	8850.25	3	2950.085	21.206 ***
0	5981.92	43	139.114	

VARIANCE COMPONENTS

LEVEL	PERCENT
1	65.51
0	34.49

DEAD CORAL

LEVEL	SS	DF	MS	Fs
1	1995.57	3	665.191	3.0903 *
0	9255.82	43	215.251	

VARIANCE COMPONENTS

LEVEL	PERCENT
1	16.42
0	83.58

SAND/RUBBLE

LEVEL	SS	DF	MS	Fs
1	3408.30	3	1136.101	4.0040 *
0	12200.76	43	283.738	

VARIANCE COMPONENTS

LEVEL	PERCENT
1	22.02
0	77.98

SIGNIFICANCE LEVEL:

$* = p < 0.05$
$*** = p < 0.001$

Table 7: Student-Newman-Keuls (SNK) test of Table 2-6 ANOVA results. Sites: PB = Punta Bejuco, PI = Punta Islotes, S = Sándalo, PEB = Punta El Bajo. Statistically similar mean values are joined by a horizontal line.

LIVE CORAL

Locality rank	1	2	3	4
Site	PB	PI	S	PEB
Means	0.96	1.71	29.08	45.87

DEAD CORAL

Locality rank	1	2	3	4
Site	PEB	PB	PI	S
Means	21.32	50.90	54.34	54.79

SAND/RUBBLE

Locality rank	1	2	3	4
Site	S	PEB	PI	PB
Means	16.13	32.81	43.95	48.12

Table 8: Shannon-Wiener diversity index (H') and species evenness (J') for the four reefs studied.

REEF	no. of species	H'	J'
Punta Islotes	1	0	0
Punta Bejuco	3	0.273	0.248
Punta El Bajo	2	0.464	0.669
Sándalo	4	0.822	0.593

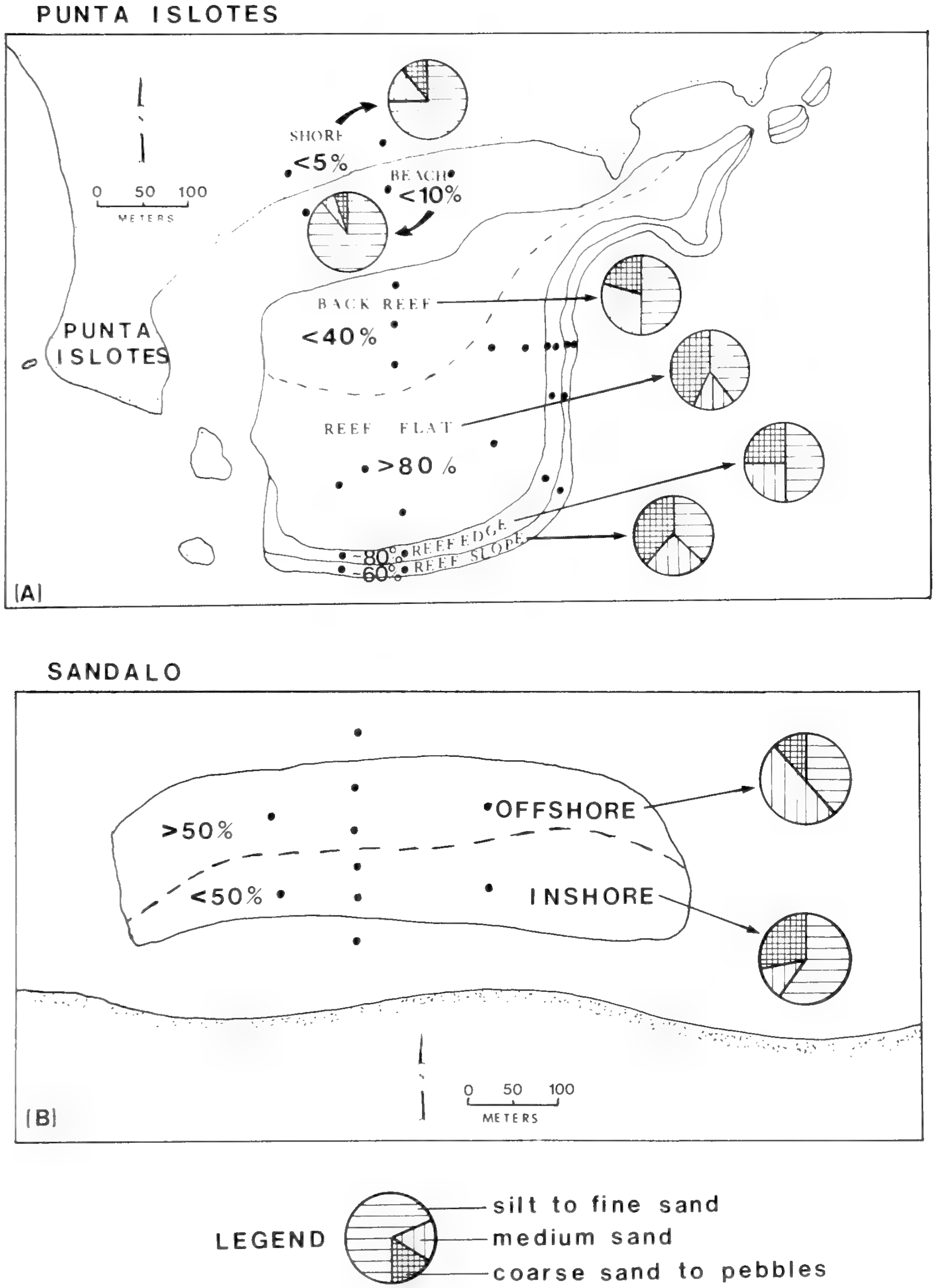

Figure 15: Percent calcium carbonate at the different reef and shore zones. Grain size distribution of the bottom sediments (percent) in the different zones is denoted by the pie diagrams. Dashed line separate the back-reef from the reef-flat at Punta Islotes (A); and the inshore from the offshore zone at Sándalo (B). Dots indicate sampling sites.

Table 9: Analysis of sediment samples from two reefs in Golfo Dulce. Average percent calcium carbonate and standard deviation in parenthesis; principal grain size(s) and main sediment components are given. See Figure 1 for location of reefs, Playitas is site number 3 on map. n = number of samples.

REEF	DEPTH	n	%$CaCO_3$	GRAIN SIZE	MAIN COMPONENTS
Playitas	1.5 m	2	54.8 (0.3)	41 % silt 26 % coarse sand-pebbles	coral and shell fragments
	2 m	2	63.8 (0.3)	70 % fine-medium sand	coral and shell fragments
Punta Bejuco	1.5 m	2	40.0 (0.5)	45 % fine-medium sand	forams and coral fragments, echinoid spines
	2 m	2	54.0 (0.5)	54 % silt-fine sand 22 % coarse sand-pebbles	coral and shell fragments
	2.5 m	2	57.7 (0.5)	67 % silt-fine sand 20 % coarse sand-pebbles	coral and shell fragments, echinoid spines
	3 m	2	77.4 (0.5)	83 % silt-fine sand	shell fragments, forams, sponge spicules

6.3 ANTHROPOGENIC DISTURBANCES

The main human activities around the Golfo Dulce area are indicated in Figure 2, and changes in the percent cover of standing primary forest in the Golfo Dulce area from 1940 – 1988 are presented in Table 10.

The watershed of the Esquinas River was the first to be altered (mid 1940's) for the cultivation of bananas. Today less than 10% of the forest is standing in the Esquinas drainage basin. The sediment-loaded waters of the Esquinas River flow south along the coast – over the area of dead coral reefs – until they merge with the main northwest circulation (Fig. 2 and 16). This pattern of circulation produces an eddy at the river's mouth and over the reefs to the west (Fig. 17).

Table 10: Percentage of standing primary forest in the Golfo Dulce area. North shore refers to the coastal area between the Esquinas River and Rincón. Punta el Bajo and Sándalo refers to the shore area adjacent to the reefs (see Figure 1 for locations). Years refers to the year the aerial photographs used for the analysis were taken.

AREA	YEAR					
	1940	1950	1961	1977	1983	1988
NORTH SHORE	100 a	100 a	100 a	100 a	30–60 b	0 d
ESQUINAS RIVER	100 a	50 a	20 a	20 a	30 b	<10 d
RINCON RIVER	100 a	100 a	100 a	100 a	90–100 b,c	90 d
TIGRE RIVER	100 a	100 a	90 a	90 a	80–90 b,c	90 d
PUNTA EL BAJO	100 a	100 a	100 a	100 a	60–90 b	90 d
SANDALO	100 a	100 a	100 a	100 a	90–100 b	90 d

REFERENCES:

a- Hartshorn et al., 1982
b- D.G.F., 1983
c- Sader and Joyce, 1988
d- D.G.F., 1989

The north shore of the inner Gulf, adjacent to the Punta Islotes and Punta Bejuco reefs, has been completely cleared in the last 10 years. As a consequence, soil erosion has increased considerably with an increase in sediment input to the marine environment (Fig. 9).

A dirt road was opened in 1983 along the north shore of Golfo Dulce. This has resulted in significant erosion in the inner sector of the Gulf' because of the road cut (Fig. 18). And has opened the area to loggers which have started to cut down the forest.

The Tigre River is an important source of terrigenous sediments to the outer Gulf area, even though 90% of the forest is still present (Table 10). The reason for this significant sedimentary input is the type of activity taking place along the course of the river. This area has been impacted recently by gold mining with river dredging, which has a limited impact on the forest canopy, but devastating effects on drainage systems (Berrangé, 1987b).

The forests of the Rincón River watershed, as well as those bordering the Sándalo and Punta El Bajo reefs, are still in fairly good condition, with 90% of the forest standing (Table 10), and are not affected by mining or other anthropogenic activities.

Figure 16: Aerial photograph of the Esquinas river near its mouth. Note the sediment plume as it encounters the main northwest current of the inner Gulf. Dead reefs are found along the shore. 9.III.1989, altitude = 300m.

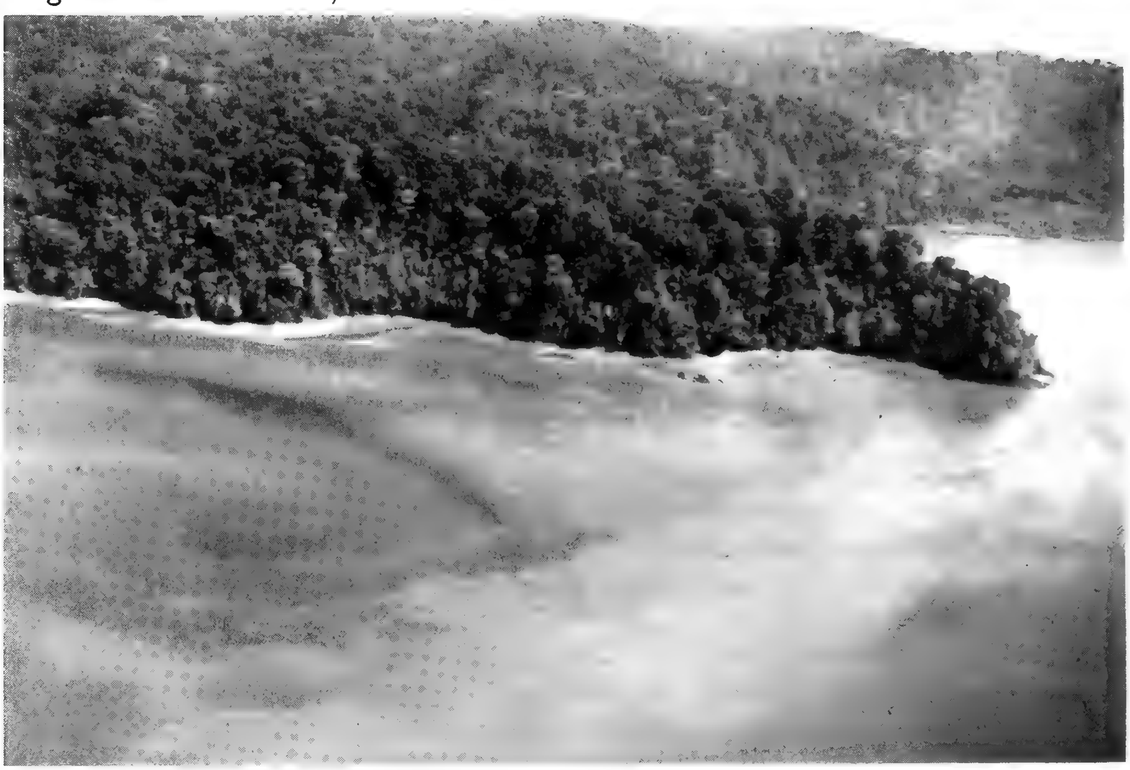

Figure 17: Eddy of sediment laden waters from the Esquinas river over a coral reef (Playitas) about 2km west of the river's mouth, 9.III.1989. Altitude = 300m.

Figure 18: Road construction near Rincón. Note the erosion of the road cut exposing the red latosol soil. Photographed in February, 1985.

7 DISCUSSION

7.1 POSSIBLE REASONS FOR INTER-REEF DIFFERENCES

7.1.1 TECTONICS

The differences in reef structure and development between the inner Gulf reefs, Punta Islotes and Punta Bejuco – thick, high topographic relief – and the outer Gulf reefs, Punta El Bajo and Sándalo – low topographic relief – may be related to differences in the tectonic regimes at the opposite ends of Golfo Dulce. Differences in the recent tectonic history of these areas have been documented from evidence of relative subsidence in several areas of Golfo Dulce, especially of the basin on the north shore (Fischer, 1980; Obando, 1986; Berrangé and Thorpe, 1988), and of uplift of the Osa Peninsula and the south Gulf shore (Berrangé and Thorpe, 1988; Bullard et al., 1988; Wells et al., 1988). The Punta El Bajo area has been identified as a zone of intense uplifting (Gardner et al., 1987). This difference in tectonic regimes may explain the thicker reef accumulations in the north Gulf, which has experienced more subsidence, than the south Gulf region.

7.1.2 SILTATION

The distribution of terrigenous sediments may explain the difference in percent live coral cover between the inner reefs and the other reefs of Golfo Dulce. The live reefs of the outer Gulf (Sándalo and Punta El Bajo) have been exposed to limited sedimentation stress. This situation contrasts with the dead reefs and the live *Porites* reefs of the inner Gulf that have

all been subjected to heavy terrigenous sediment concentrations associated with the outflow of the Esquinas River (Fig. 2) and landslides on the coastal area adjacent to the reefs (Fig. 9). The Esquinas River, which drains deforested mountains and agricultural and cattle land (Table 10), carries heavy sediment loads during the long rainy season (Fig. 16). In addition, flooding has increased in recent years, probably due to deforestation as demonstrated for others areas by Clark (1987). More recently, the construction of a road through the Osa Forest Reserve on the north shore (Fig. 18), together with accelerated deforestation of the steep shore areas (Table 10), have contributed significantly to the siltation problem. It has been demonstrated that trees near the shore regulate the input of sediments and nutrients to near-shore environments (Kühlmann, 1985). In this context, it is worth noting that the coastal forests adjacent to the Punta El Bajo and Sándalo live reefs are still relatively undisturbed (Table 10).

A similar distribution of living reefs in relation to sedimentation patterns was found by Roberts and Murray (1983) on the Caribbean shelf of Nicaragua. No reefs were found in near-shore turbid environments and most coral reef development was restricted to clear waters at the shelf edge. On the Nicaraguan shelf edge, the percentage of carbonate sediments was 80% or more (Roberts and Murray, 1983) – this contrasts with the low values of calcium carbonate for Golfo Dulce sediments. These Gulf values were in the lower range of high-carbonate facies of the Great Barrier Reef (Maxwell, 1973) and were similar to the values obtained from near-shore terrigenous environments on the Miskito Bank, Nicaragua (Roberts and Murray, 1983). Acevedo et al. (1989) observed that in southern Puerto Rico live coral cover and species diversity increased away from a terrigenous sediment source.

Water circulation within the Gulf appears to be counter-clockwise, i.e., there is a general flow into the Gulf along the eastern and northern shore and an outward flow along the western and southern shore (Fig. 2). This pattern of water movement will transport sediments from the Esquinas River into the area of the inner Gulf reefs and away from Punta El Bajo reef, which is not influenced by any other large river. The waters of the Rincón River, which drain pristine forests, north-west of the Sándalo reef, generally have low sediment loads. As a result, no significant amount of sediment is transported to the Sándalo area. Also, sediments from the Tigre River, to the east of the Sándalo reef, are transported away from the reef by the counter-clockwise currents (Fig. 2). This pattern is probably the reason why a *Pocillopora* reef, east of Sándalo, observed alive in 1978 (P. W. Glynn, per. comm., 1985) was found covered with mud – only the tallest colonies could be seen – in February 1985. This reef was probably killed by the severe floods of 1984 (Cortés and Murillo, 1985) in the mining area of the Osa Peninsula (Berrangé, 1987b).

Siltation may be the main cause of coral reef demise worldwide (Johannes, 1975; Rogers, 1985, 1990; Wells, 1986; Kühlmann, 1988; UNEP/IUCN, 1988). It has been demonstrated that high sediment loads around coral reefs can cause a reduction in coral species diversity and live coral coverage, and alterations in coral species composition and distribution (Loya, 1976; Cortés and Risk, 1985; Hubbard, 1986; Rogers, 1990) and, ultimately, coral death (Bak, 1978; Rogers, 1979; 1983; Thompson et al., 1980). The coral reefs of Golfo Dulce show all the signs of siltation stress – low live coral cover and species diversity, and high dead coral cover and concentrations of terrigenous sediments – especially the reefs in the inner Gulf area. Coral reefs near the Esquinas River are all dead and those farther away are in a state of decline.

7.2 OTHER CAUSES OF CORAL DEMISE

In addition to the stress caused by high sediment loads, other factors may have played a role in the demise of corals in Golfo Dulce reefs: coral collecting, low salinity, high sea surface temperature and phytoplankton blooms. These factors are discussed below and their impacts on Golfo Dulce corals are evaluated.

Several people interviewed around Golfo Dulce stated that there has been extensive collecting of coral colonies in the recent past, especially *Pocillopora damicornis*. But this does not seem to be a significant factor because many fragments of dead *Pocillopora* were found at all reefs, and at Punta Islotes large areas of the reef were covered with dead *Pocillopora* in growth position.

Golfo Dulce is located in one of the wettest regions of Costa Rica and four large rivers flow into it. During the rainy season a fresh water lens forms and it is very persistent, salinity may drop to 25ppt (M. L. Fournier, pers. comm., 1990). Moreover, the Spanish name of the Gulf implies the presence of fresh water (Golfo Dulce = Fresh Water Gulf). Two lines of evidence indicate that salinity may not be an important factor in the demise of the Golfo Dulce coral reefs. First, the surface salinity of Golfo Dulce during the dry season ranged from 30 to 32ppt (Richards et al., 1971; Kuntz et al., 1973), and may drop to 25ppt during the rainy season (M. L. Fournier, pers. comm., 1990). These values above or close to the generally accepted low salinity tolerance limit (<27ppt) for corals (Wells, 1956). Second, experimental evidence and laboratory observations indicate that some species of corals are tolerant to pronounced salinity changes. Muthiga and Szmant (1987) demonstrated a high tolerance of salinity change by *Siderastrea siderea*. Glynn (1974) indicated that eastern Pacific corals remained healthy in aquaria during the wet season in Panama, when salinities dropped below 25ppt and even reached 19ppt on two occasions.

In recent years there have been reports of extensive coral mortality in the eastern Pacific: in 1983 due to high and prolonged sea surface temperatures that accompanied a severe El Niño event (Glynn, 1984; 1988a; 1990; Glynn et al., 1988), and in 1985 in association with dinoflagellate blooms (Guzmán et al., 1990). Unfortunately, there are no quantitative data from Golfo Dulce before the 1982-1983 El Niño to evaluate the impact of the warm water as a possible factor in the demise of Golfo Dulce reefs. However, in Golfo Dulce coral mortality does not seem to have been as intense as in other eastern Pacific reefs (Glynn, 1990). One reason for this may be that most of the Golfo Dulce corals were dead prior to 1982, especially *Pocillopora damicornis* that was the most affected in the eastern Pacific (Glynn et al., 1988).

In 1985, intense dinoflagellate blooms caused coral mortality in several eastern Pacific reefs (Guzmán et al., 1990). At Golfo Dulce, during that same period, intense blooms were observed, but their effects may not be significant since the main genera affected elsewhere, *Pocillopora*, was dead prior to 1985.

7.3 COMPARISON WITH OTHER EASTERN PACIFIC REEFS

The coral species associated with the Golfo Dulce reefs (Table 2-1) are characteristic of eastern Pacific reefs (Wells, 1983). The Golfo Dulce reefs, however, lack some common eastern Pacific corals including *Pocillopora elegans* Dana, *Pavona clavus* Dana and *Gardineroseris planulata* (Dana).

In contrast to most eastern Pacific coral reefs (e.g., Panamá: Glynn et al., 1972; Gorgona Island, Colombia: Glynn et al., 1982; Prahl and Erhardt, 1985; Los Frailes Bay, Baja

California: Glynn and Wellington, 1983; and some reefs in the Galápagos Islands: Glynn and Wellington, 1983), with large portions composed of pocilloporid framework, the Golfo Dulce reefs are constructed chiefly by poritid coral frameworks. Other coral communities, for example, in the Sea of Cortés (Squire, 1959; Brusca and Thomson, 1975), off some islands in the Galápagos (Glynn and Wellington, 1983) and off the Costa Rican mainland coast (Glynn et al., 1983; Cortés and Murillo, 1985) are composed of sparse populations of both pocilloporid and massive corals. At Caño Island, Costa Rica, *Porites lobata* is the main reef building coral (Guzmán, 1986; Guzmán and Cortés, 1989a), as well as in some areas at Malpelo Island, Colombia (Birkeland et al., 1975) and Cocos Island (Bakus, 1975; Guzmán and Cortés, in review). On the inner reefs of Golfo Dulce, *Porites lobata* is also the predominant species, but there it forms extensive monospecific stands on the reef-edge and slope with a pocilloporid reef-flat located behind the reef-front.

Porites lobata is sometimes the only species alive at some reef sites in Golfo Dulce, suggesting that it is the most tolerant coral to physical disturbances. Massive *Porites* species have been reported to be the dominant corals on the inner shelf reefs of the Great Barrier Reef (Done, 1982). Indeed, *Porites lobata* is the predominant species at Pandora reef, an inner shelf reef of the Great Barrier Reef, in terms of physical mass, amount of living tissue and colony number (Potts et al., 1985). The inner shelf of the Great Barrier Reef is characterized by low water transparency, low wave action and the presence of terrigenous silicates and silts (Done, 1982) – similar to conditions associated with Golfo Dulce reefs. *Porites lobata* is a very hardy species, and at Caño Island its predominance was attributed to its resistance to environmental fluctuations, frequent asexual reproduction by fragmentation, as well as sexual reproduction, high rate of wound recovery, and low levels of predation (Guzmán, 1988; Guzmán and Cortés, 1989a,b). As at Caño Island, *Porites lobata* in Golfo Dulce reproduces by fragmentation caused by the feeding of the triggerfish *Pseudobalistid naufragium* on the boring bivalve *Lithophaga* spp. (H. M. Guzmán, pers. comm., 1989), and probably also by sexual means. It is exposed to low levels of predation since *Acanthaster planci* (Linnaeus) and *Phestilla* sp., two predators of *P. lobata* (Glynn, 1974, 1976; Hadfield, 1976; R. C. Highsmith, pers. comm. in Glynn, 1982; Guzmán, 1988) have not been found in Golfo Dulce.

There is little echinoid bioerosion taking place on the Golfo Dulce reefs. Spines of the sea urchin *Eucidaris* sp., an important carbonate bioeroder in the Galápagos Islands (Glynn et al., 1979; Glynn, 1988b), are found in the sediments, but live animals have not been seen in Golfo Dulce. In addition, very few *Diadema mexicanum* A. Agassiz, another important bioeroder in the eastern Pacific (Glynn, 1988b; Guzmán and Cortés, in review), have been observed in Golfo Dulce. By contrast, internal bioerosion appears to be important (Cortés, in prep.), especially by the boring bivalves *Lithophaga* spp. and *Gastrochaena rugulosa*, a boring sponge *Cliona ensifera* and a coral boring shrimp *Upogebia rugosa*.

8 CONCLUSION

Environmental conditions for coral growth in the Golfo Dulce area have been deteriorating since the 1940's, coinciding with the initiation of extensive deforestation. The size of the reefs and the abundances of dead corals indicate that environmental conditions were more conducive to reef growth in the recent past. The increase in sediment loads, caused by deforestation, deleterious agricultural practices, road construction and mining activity, may be the main sources of stress on the Golfo Dulce reefs.

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NO. 345

HETEROPTERA OF ALDABRA ATOLL AND NEARBY ISLANDS, WESTERN INDIAN OCEAN, PART 1. MARINE HETEROPTERA (INSECTA); GERRIDAE, VELIIDAE, HERMATOBATIDAE, SALDIDAE AND OMANIIDAE, WITH NOTES ON ECOLOGY AND INSULAR ZOOGEOGRAPHY

BY

D. A. POLHEMUS

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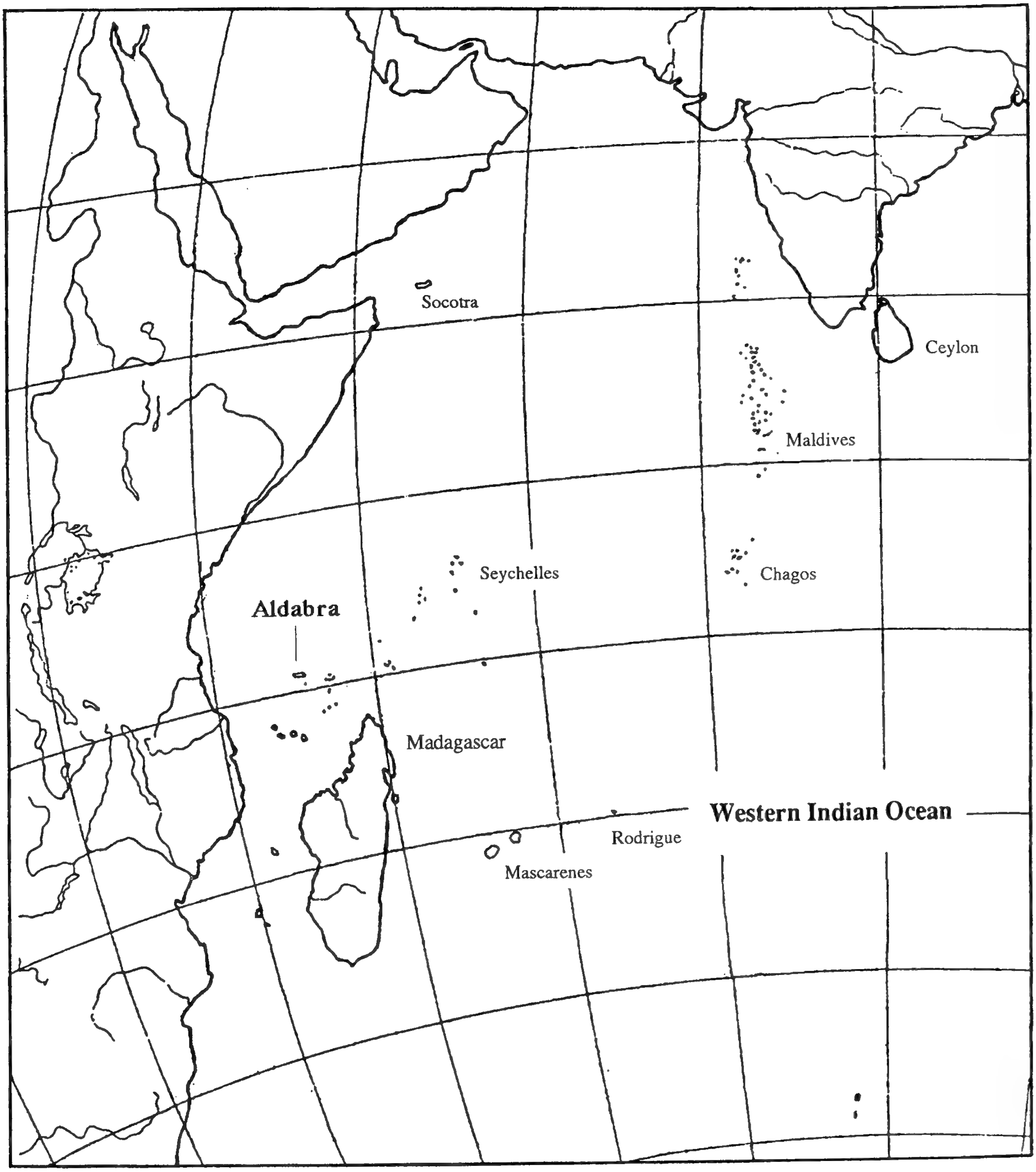
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BY

DAN A. POLHEMUS

ABSTRACT

Ten species of Heteroptera are now known from marine habitats at Aldabra and Cosmoledo atolls. Nine of these species, *Halobates micans*, *Halobates germanus*, *Halobates flaviventris*, *Halobates alluaudi*, *Halobates poseidon*, *Hermatobates djiboutensis*, *Halovelia seychellensis*, *Salduncula seychellensis*, and *Corallocoris aldabrae* are marine obligates, while one, *Microvelia diluta diluta* is a primarily freshwater species that appears to have opportunistically colonized tidally flooded sinkholes. The distributions of the marine species are not homogenous around Aldabra, but are instead divided among three distinct zones: the exposed seaward shores on the eastern and southern coasts, the sheltered seaward shores on the western and northern coasts, and the lagoon. These areas harbor distinctive species assemblages whose composition is based on the ecological preferences of the individual species involved. It is hypothesized that the effects of the strong southeast monsoon have led to a richer assemblage of species on the leeward side of the island. A key to all marine species is provided, accompanied by maps detailing their distributions on Aldabra.

INTRODUCTION

This report presents the systematic results of an intensive sampling program concentrating on Heteroptera in marine habitats at Aldabra atoll (9° 24' S, 46° 20' E), from March 5 to March 25, 1989. Additional smaller collections were also made at Cosmoledo atoll (9° 41' S, 47° 35' E) during the return trip from Aldabra, and since the faunas of the two islands are nearly identical the results of the Cosmoledo collections are included in this report as well.

This work is divided into two sections. The first deals with the ecological preferences and local zoogeographical patterns exhibited by marine Heteroptera on Aldabra atoll. The second part contains a systematic treatment and distributional records for the individual species involved. Additional information on the systematics of *Halobates* species occurring on Aldabra and nearby atolls may be found in Polhemus and Polhemus (in press). Chapters dealing with all the marine groups treated herein, with information on their biology and ecology, may be found in *Marine Insects*, edited by Cheng (1976).

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All the collections discussed below were made by the author, primarily through the use of hand held dip nets with 45 cm. diameter hoops. Similar nets were skimmed along the water surface from boats during circuits around the outer rim of the island and in transits across the lagoon; collections made in this latter fashion are referred to as net tows in the subsequent discussions. All specimens are held in the collections of the Department of Entomology, Smithsonian Institution, Washington, D. C. (USNM) and the J. T. Polhemus collection, Englewood, Colorado (JTPC). CL numbers following localities refer to a code used by the author to reference ecological data. A detailed map of Aldabra atoll showing the localities discussed herein may be found in Stoddart and Westoff (1979). The individual islets making up the outer rings of Aldabra and Cosmoledo atolls are noted in bold face in the material examined sections. Latitudes and longitudes were determined using a Satnav global positioning system.

ECOLOGY

Habitat

Stoddart (1967) classified Aldabra as an elevated atoll, raised several meters above present sea level and occupying an ancient volcanic platform with steeply plunging outer slopes. The island is ring-like, formed in the shape of an elongate oval with the long axis oriented east-west. Its length is approximately 34 kilometers, and its maximum width 15 kilometers. The outer rim consists of 18,800 hectares of dry land and 2000 hectares of mangroves enclosing a lagoon of 14,200 hectares, and is broken by four passes on the western and northern sides; these are, clockwise from the west, the Passe Femme, Grande Passe, Passe Gionnet and Passe Houareau. All of these passes are relatively deep, with the Grande Passe having a maximum depth of 24 meters (79 feet) at its entrance, while the lagoon is shallow, averaging only 2 to 3 meters (6.5 to 10 feet) in depth at low tide. The tidal range at Aldabra is high, reaching 2.6 meters (8.5 feet) on the outer coasts. Due to the relatively small size of the passes in relation to the area of the lagoon the tidal lag between the sea and the more remote portions of the lagoon may be 4 to 5 hours, and current velocities in the passes can reach 6 meters per second.

Aldabra lies in the driest sector of the western Indian Ocean, receiving an annual rainfall of about 940 mm. per year (Stoddard and Mole, 1977). The majority of this rainfall occurs between late November and April, when the island is under the influence of the northwest monsoon, which reaches its height in January and February. During the remainder of the year, from May to early November, the island is swept by the relatively dry southeast monsoon. The two wind regimes are not equivalent; the northwest monsoon winds tend to be lighter and more intermittent, with occasional heavy storms, while the southeast monsoon winds are strong and steady, frequently attaining velocities between 10 and 20 knots. As a result, sea conditions are considerably rougher during the southeast monsoon, and the exposed southern and eastern coasts of the atoll are heavily battered by waves at this time of year.

Due to its isolation and lack of human disturbance, Aldabra harbors one of the most diverse assemblages of marine Heteroptera known on Earth. The structure of the atoll and its consequent variety of habitats, in particular the configuration of the shore and the reefs immediately offshore, has had a marked effect on the distribution of these insects. Based on my collections at Aldabra, the following enviromental divisions are perceived to be particularly important to the marine Heteroptera, and are referred to in the subsequent discussions:

A. Fore reef: this is interpreted as the section of the fringing reef sloping seaward from the tidally exposed reef crest or from the shore platform in areas where the reef crest

is lacking. It is essentially unprotected from the effects of wind and surf coming in off the surrounding open ocean.

B. Reef crest: this term refers herein to the offshore portion of the fringing reef exposed at low tide. Reef crests are well developed on the western and northern sides of Aldabra along Picard, Polymnie and Malabar islands, but essentially absent on the eastern and southern sides of Grande Terre island from Point Hodoul to Pointe aux Vaqua, except for a small section of platform reef in the bight east of Dune Jean Louis.

C. Back reef: this is the section of the reef lying between the reef crest and the shore. It is generally present in the form of a shallow lagoon with a floor of coral rubble or sand, and in many places, such as in the vicinity of the research station, is exposed at low tide. In areas where a reef crest is lacking the back reef environment is also absent.

D. Seaward shore: this is the actual outer shore of the island proper, and may take several forms. At the reseach station and in a few other isolated coves or "anses" it is composed of a beach of fine white coralline sand. More typically it is a vertical or undercut jagged limestone cliff dropping directly to the water, as seen along nearly the entire seaward coast of Malabar and Polymnie. At other points, particularly on the eastern and southern coasts of Grande Terre, this cliff may be low and fronted by a sloping shelf of relatively smooth limestone the runs out under the sea but is exposed at low tide. These three types of seaward shores are referred to as sandy, vertical, and sloping respectively.

E. Passes: these are the channels by which the waters of the lagoon communicate with the open ocean. They have strong tidal fluxes that give them the characteristics analogous to flowing rivers in freshwater systems. Their shores are primarily vertical cliffs.

F. Mangroves: refers to the fringing mangrove estuaries that surround much of the inner lagoon. These are composed primarily of *Avicennia marina* and *Rhizophora mucronata* in the eastern end of the lagoon, while a small patch of *Sonneratia alba* occurs just inside the Passe Femme at the western end. Mangroves on Aldabra are entirely confined to the shores of the lagoon except for a small stand in the extremely protected cove at Au Park on the seaward shore of Malabar.

G. Lagoon: this term refers to the inner lagoon beyond the mangrove estuaries. The waters of the lagoon are relatively calm in comparison to the open ocean, although a swell may form from wind action. The floor of the lagoon is primarily white sand in the central section and carbonate mud at the eastern and western ends.

H. Lagoon islets: these are small detached limestone islets, frequently circular in shape, with sides strongly undercut by wave and tidal action. Typically they attain a mushroom-like form with the upper limit of undercutting lying at the high tide line.

I. Bassins: this term applies to small to large limestone sinkholes in the interiors of the islands making up the outer rim, particularly Picard. These sinkholes are connected with the sea through subterranean passages and are flooded with seawater, usually permanently but in some cases only at high tide. Many such bassins are present behind the research station, including Bassin Lebine, Bassin Cabri, and the Upsidedown Jellyfish Pool.

Local Distribution of Genera and Species

Hermatobates: Foster (1989) studied the biology of *Hermatobates weddi* on Fiji, and found that the insects occurred primarily along the reef crest, emerging at low tide from their hiding places amid air pockets in coral rubble to forage on the calm pools formed on the reef crest itself or on protected areas of water immediately seaward. Essentially the same pattern was reported by Cheng (1977) for species on New Caledonia and the Great Barrier Reef of Australia, and by J. Polhemus (1982) for *H. haddoni* at Darwin, along the coast of the Arafura Sea. In addition, I have observed similar behavior

among *Hermatobates* species occurring on the island of Sumbawa in the Lesser Sunda chain of Indonesia, and on Malupore Island off the southeastern coast of New Guinea. At Aldabra, however, the *Hermatobates* species present, *H. djiboutensis*, displayed a markedly different behavior pattern. Adults and late instar immatures were nearly absent on the reef crest, but instead were typically encountered in the deep water over the fore reef between 500 and 1000 meters offshore, in areas subject to moderate swell. Here they would run across the surface of the sea in company with various *Halobates* species, and could be captured by trolling a net from the bow of a moving boat. Individuals appeared to be more abundant in areas where seaweed and other organic debris formed loose floating mats on the water surface. The presence of *Hermatobates* did not appear to be correlated with tide stage, since captures were made at both low and high tides, and all captures were made during daylight hours, even though Usinger and Herring (1957), Cheng and Leis (1980), and Cheng and Schmitt (1982) have suggested on the basis of circumstantial evidence that *Hermatobates* forage primarily at night.

In contrast to the adults, immatures in early developmental stages (instars I - III) were encountered only in reef crest habitats at low tide. In addition, the only mating pair of adults captured was taken on the reef crest offshore of the research station at dead low tide. It thus appears that mating, oviposition, and early maturation of this species at Aldabra occur on the reef crest, as is typical for *Hermatobates* in other regions, but that adults and late instar immatures then forage seaward of the reef crest on the deep waters over the fore reef and do not necessarily return to hiding places in the coral blocks at high tide, a behavior pattern not previously reported. *H. djiboutensis* was found at Aldabra only in areas with well developed reef crests, these being primarily on the western and northern sides of the island, plus the small sheltered area on the south coast of Grande Terre near Anse Vaqua. This distribution is shown in figure 1. The restriction of this species to areas with reef crests is further evidence supporting the hypothesis that such habitats are necessary as oviposition sites and refugia for immatures.

These observations contradict previous conclusions and generalizations about adult *Hermatobates* behavior derived by Esaki (1947), Usinger and Herring (1957), Cheng (1977), and Foster (1989) from observations on populations in the western Pacific. Several factors may be responsible for this. Since the observations at Aldabra were made in March, during the calm period between the northwest and southeast monsoons, it is possible that the behavior patterns recorded may be seasonal, and that during times of the year when the sea surface is more constantly disrupted the insects forage nearer the reef crest. On the other hand, it may also be that *H. djiboutensis* possess different foraging patterns than other Indo-Pacific *Hermatobates* species. This latter hypothesis must be investigated more critically, since I have also observed *H. djiboutensis* on Mauritius where it exhibited the "typical" *Hermatobates* behavior pattern, emerging from coral rubble at low tide and skating on shallow back reef waters at Big Black River Bay. Further investigations on the ecology of this and other species will be necessary to resolve such questions, and to understand why presently accepted concepts of adult *Hermatobates* behavior are inapplicable to *H. djiboutensis* at Aldabra.

Halobates: Five species of *Halobates* were collected at Aldabra during the present survey. Two of these, *H. micans* and *H. germanus*, belong to a pelagic group of species which occur solely in open ocean habitats and do not generally approach closely to land. By contrast, the three remaining species, *H. flaviventris*, *H. alluaudi*, and *H. poseidon*, belong to the nearshore species group, members of which are restricted to coastal habitats and do not forage far onto open waters. This basic division of ecological preferences has important consequences for the distribution of these species at Aldabra.

The two oceanic species, *H. micans* and *H. germanus*, were encountered only 1000 meters or more offshore, either over the fore reef or on the deeper ocean beyond; they were never seen over the reef crest and back reef or in the lagoon (see figs. 2 and 3).

These were the only two species of *Halobates* present offshore of the eastern and southern coasts of the island, which have vertical or sloping seaward shores exposed to the full force of the southeast monsoon and lacking major reef crest and back reef development. The two species were often taken sympatrically and did not appear to partition the ocean environment in any fashion.

By contrast, the three nearshore species showed distinct segregation of habitats. *H. flaviventris* was most typically encountered over the fore reef 500 to 1000 meters offshore, often in company with *Hermatobates djiboutensis*. It was not seen inshore of the reef crest in the back reef, passes, or in the lagoon (see fig. 3). Individuals were widely separated, appearing to forage independently, and this species was never observed forming schools. Typically only one or two specimens would be taken in a net tow for every ten or twenty *H. alluadi* captured. In its behavior *H. flaviventris* appeared to be intermediate between the strictly open ocean species and those confined to nearshore habitats. Its tendancy to cruise over fore reef waters parallel to the reef crest was similar to the behavior pattern observed for *H. princeps* White in the Malay Archipelago.

H. alluaudi was sympatric with *H. flaviventris* in the vicinity of the reef crest and over the fore reef just beyond, but was more typically found inside the reef crest skating over the back reef lagoon adjacent to sandy or vertical seaward shores, and was almost never seen more than 1000 meters offshore. It was also common along the margins of the lagoon, primarily in the vicinity of the passes or the rocky lagoon islets, but here again it was absent from the central lagoon more than 1000 meters offshore (see fig. 4). *H. alluaudi* is a fast, powerful and agile swimmer, and at Passe Femme and Passe Gionnet individuals of this species were observed holding station along the channel margins against the incoming tide, thus foraging in place as the tidal flux washed past them in a manner analogous to that seen among freshwater Gerridae on flowing streams. This species occasionally formed small schools in sheltered spots at low tide, but for the most part appeared to be relatively well dispersed on the water and not exceptionally social.

H. poseidon was found only in conjunction with mangroves, and was thus almost entirely confined to the margins of the lagoon. Individuals were also present in several flooded limestone sinkholes on Picard Island. This species, which does not swim with nearly the same speed or power as *H. alluaudi* or *H. flaviventris*, was never seen more than 500 meters offshore, and usually stayed within the shelter of the mangrove estuaries (see fig. 5). This was the only *Halobates* species on Aldabra to typically occur in large schools during all tide stages, and many mating pairs were observed. In many aspects its behavior appeared similar to that reported for *H. fijiensis* by Foster and Treherne (1986), which was studied on Fiji and also found to be restricted to the mangrove and back reef zones.

Because of these habitat preferences, the central section of the lagoon was basically devoid of *Halobates*. The two nearshore species along the lagoon margins, *H. poseidon* and *H. alluaudi*, did not stray far enough from shore to reach the mid-lagoon waters. By contrast, the remaining species, which have habits that would allow them to exploit these areas far from shore, seemed to be unwilling to enter the narrow passes connecting the lagoon with the ocean beyond, and were therefore confined solely to the outside of the atoll. It thus appears that the combination of aversion to open waters on the part of some species and aversion to shoreline proximity on the part of others leaves the central lagoon essentially unexploited by *Halobates*. The only individuals ever seen here were a few stray individuals of *H. alluaudi* which had apparently been carried inward on the strong tidal flux from the Grande Passe during the high tide filling cycle.

Also notable was the absence of any nearshore *Halobates* species from the seaward shores on the southern and eastern sides of the atoll, a pattern analogous to that seen in the previously discussed *Hermatobates djiboutensis*. This seems to be due to the effects of the southeast monsoon, which batters these coasts with extremely heavy wind and seas for

nearly half of each year, from June through October. Foster and Treherne (1986) found that strong onshore winds had a marked effect on the distribution of *Halobates fijiensis* in Fiji, and at Aldabra it also appears that the combination of rough wind-driven seas and a shoreline lacking refuge space in the form of a reef crest or back reef effectively excludes the nearshore *Halobates* species from these exposed sections of the atoll.

In addition to providing oviposition sites and shelter from wave action, shoreline features were also used by *Halobates* to escape the effects of the equatorial sun. When low tides occurred during the middle of the day large sand flats were exposed along the inner margin of the lagoon inside of the Passe Femme. Rising from these flats were lagoon islets of various sizes, all undercut and sheltering pools of seawater at their bases. These shaded pools were the low tide retreats for vast schools of *Halobates poseidon* and *Halobates alluaudi*, which occurred in mixed species assemblages containing both adults and immatures. These schools were seen only on shaded pools beneath the overhanging lips of the lagoon islets, primarily on the sides of the islets receiving a cooling breeze, and were absent on nearby pools of similar size and depth that were unsheltered and open to the full force of the sun. In such unsheltered pools the water temperature exceeded 40° C., which was clearly intolerable to *Halobates*, while in the sheltered pools the seawater temperature was 28-30° C. The afternoon low tides thus forced these two species into temporary sympatric assemblages of abnormal density in shady refugia, from which they then dispersed upon the subsequent turn of the tide.

Finally, there is the question of how populations of *H. poseidon* and other marine Heteroptera became established in the bassins of Picard Island. Since many of these bassins are connected to the sea only via completely water filled subterranean passages it seems unlikely that the colonization was effected by adults or immatures merely swimming or floating in on the tides. Instead, it seems that the bassins represent isolated pockets of marine habitat that have been colonized by chance dispersals, a hypothesis supported by several observations. All the bassins sampled contained one of the three following species of marine Heteroptera: *Halovelia seychellensis*, *Microvelia diluta*, or *Halobates poseidon*. It is important to note, however, that no individual bassin contained more than one of these species. *H. poseidon*, for instance, was found in only two of the many bassins sampled, the Upsidedown Jellyfish Pool and Bassin Lebine, and in these bassins no other marine Heteroptera species occurred. In Bassin Cabri only *Halovelia seychellensis* was present, and in another small bassin behind the research station only *Microvelia diluta*. This suggests that whichever species of surface dwelling Heteroptera is first able to colonize a given bassin is subsequently able to dominate it and to exclude other invading species, and that colonization of the bassins has proceeded in a haphazard fashion. *M. diluta* produces a percentage of winged adults in each generation and would thus intuitively seem to have an edge in colonizing the bassins, but in fact it is present in only approximately one third of them. The other two species involved do not produce winged individuals and must have reached the bassins by other means. This colonization may have been accomplished by various agencies, including wind dispersal of adults or immatures during storms, similar storm mediated transport of eggs laid on floating debris, or transport of eggs on the feet or feathers of sea birds.

Halovelia: A single species of *Halovelia*, *H. seychellensis*, was present on Aldabra, but it occupied a wide variety of habitats. Individuals were most typically encountered along vertical seaward shores sheltered by a reef crest and back reef; in these locations they would skate at low tide on small pools which formed amid coral rubble which had fallen from the cliffs or eroded from the reef crest. This behavior pattern is very similar to that reported by Andersen (1989) for *H. malaya* on Phuket Island, Thailand, and also close to that described by Kellen (1959) for *H. bergrothi* (as *H. marianarum*), which occurred among volcanic rocks bordering an artifical lagoon in Samoa. On Aldabra moderate numbers of *H. seychellensis* were also found just north of

the research station where several long ridges of wave-smoothed limestone ran obliquely into the back reef lagoon, creating elongate rock rimmed pools at low tide. As discussed above, this species was also present in several limestone sinkholes on Picard isiand, notably Bassin Cabri and several other nearby pools that are connected by a common cavern system. The insects generally stayed near the margins of these sinkholes, and retreated beneath rock overhangs at the onset of rain squalls. Despite their small size and general preference for nearshore habitats, stray individuals of *H. seychellensis* were occasionally taken up to 500 meters offshore, along both the outer margin of the atoll and in the lagoon.

Salduncula: The intertidal saldid *Salduncula seychellensis* was found only on sloping seaward shores along the southern and eastern coasts of the atoll in areas heavily battered by the southeast monsoon. In these areas a broad pediment of relatively smooth limestone exposed at low tide slopes gently upward to a narrow beach. This beach in turn fronts a low but jagged cliff that marks the limit of the intertidal zone. *S. seychellensis* was found only on this cliff, being absent on the narrow beach, sloping pediment, and other isolated limestone prominences separated from the cliff but connected with the shore at low tide. Immatures of all instars and adults emerged with the falling tide from hiding places amid the porous limestone rock of the cliff face and foraged over its surface. The insects moved slowly if left alone, but if pursued the adults were quick to fly, while the immatures would head for the shelter of small crevices or cavities in the rock. Individuals of *S. seychellensis* would continue to forage even after the tide had turned, waiting until the cliffs began to receive spray from breaking waves before returning to their hiding places in the rocks.

At Cosmoledo atoll this species was found in a somewhat different situation near the Johannes Point settlement on Menai island. Here the insects occurred on large blocks of coral rubble bordering the back reef lagoon. This indicates that the apparent preference for wave swept shores on Aldabra may be misleading, and that this unobtrusive species may in fact be distributed around the entire seaward shore of the latter atoll.

Corallocoris: Dwarf coral bugs belonging to the species *Corallocoris aldabrae* are known from a single locality on Aldabra: the western margin of the Passe Houareau near Middle Camp. The insects were found here at low tide running on and within a collection of rounded 3-6 centimeter long coral cobbles lying on top of a bed of firm sand adjacent to a sloping exposure of limestone at the high tide line. They appeared to be very localized in their occurrence, since a search of other similar looking sites nearby in the same cove and several other adjacent coves produced no trace of them, nor were they found in other similar habitats on other parts of the atoll even after diligent searching.

Individuals of *C. aldabrae* were not easy to collect, due to their small size and considerable jumping ability; the most successful method involved slowly removing the coral cobbles and watching for the small black insects as they hopped away across the white sand, then sucking them into an aspirator. When pursued the insects would spring away, or seek the shelter of pockets, holes and overhangs in the cobbles and limestone shelf rock. The present observations would indicate that this species forages interstitially within the cobble beds, which may account for its difficulty of detection and capture.

This habitat is quite different than that reported for *Omania naruensis* by Herring and Chapman (1967), who found the insects in the interstices of coral pinnacles in the back reef lagoon on Nauru, or for *Omania marksae* which has been taken from coral boulders in the back reef lagoon on Kwajalein atoll (A. R. Gillogly, pers. comm.). It is however, similar to the habitat in which J. T. Polhemus and I have taken *Omania marksae* in Singapore, where the insects occurred amid beach drift and coral cobbles adjacent to an exposed ridge of limestone beach rock. Kellen (1960) also reported *Corallocoris samoensis* from a beach of volcanic rocks bordering a lagoon in Samoa, although these rocks were much larger than the small coral cobbles that formed *Corallocoris* habitat on

Aldabra. As with *Hermatobates*, it appears that the behavior patterns and habitat preferences of Omaniidae are not uniform throughout the Indo-Pacific, even within individual species.

Microvelia: Although basically a freshwater species, *Microvelia diluta* was taken from several tidally flooded limestone sinkholes on Picard island which can be rightfully considered marine habitats, since they fill with salt water on a diurnal basis and harbor chitons on their walls. The insects ran about and aggregated on the open water surface at high tide when the sinkholes were innundated, then foraged on the damp mud and rock floors of the sinkholes during low tide when the water drained out. This same species was also an opportunistic colonist of freshwater habitats throughout the atoll, including temporary rainwater pools in limestone, rain barrels, and covered water cisterns.

Summary

Although at first glance Aldabra might seem a relatively homogenous environment for marine Heteroptera, the collections made during the present survey clearly indicate that the species present are not uniformly distributed around the atoll. Instead they occupy three major zones: a.) the exposed outer coast (the eastern and southern seaward shores which are swept by the full force of the southeast monsoon and lack an offshore reef crest); b.) the sheltered outer coast (the western and northern seaward shores which are protected from the southeast monsoon and have a well developed reef crest, plus the sheltered indentation on the south coast near Anse Vaqua); and c.) the lagoon. The exposed outer coast is the poorest in terms of species, harboring only the two pelagic *Halobates, H. micans* and *H. germanus*, plus the intertidal saldid *Salduncula seychellensis* which appears to be restricted to it (figs. 2, 3, 8). In contrast, the sheltered outer coast supports the most species, and is essentially the only area in which *Hermatobates djiboutensis, Halobates flaviventris*, and *Corallocoris aldabrae* are found (figs. 1, 4, 9). The lagoon is relatively species poor, but is the primary habitat of the mangrove associated *Halobates poseidon* (fig. 6). Both of the latter two zones share *Halobates alluaudi* and *Halovelia seychellensis* (figs. 5, 7), which appear to make little distinction between them. It thus appears that the strong southeast monsoon, either through its immediate actions of wind and surf or via its effects on the topography of the shoreline, has produced a marked habitat partitioning among the marine Heteroptera of Aldabra.

In addition to these patterns, we see the unusual occurrence of three species, *Halovelia seychellensis, Microvelia diluta*, and *Halobates poseidon*, in the limestone bassins of Picard Island. Such colonization of flooded cave systems by marine Heteroptera has not been previously reported from other atolls, although the author and J. T. Polhemus took *Halovelia depressa* from a similar seaside limestone sinkhole in southwestern Madagascar (see discussion in Andersen, 1989).

SYSTEMATICS

KEY TO THE ADULTS OF SPECIES OF OBLIGATELY MARINE HETEROPTERA OCCURRING ON ALDABRA AND COSMOLEDO ATOLLS

1. a. Wings always present, although often coleopteriform; semiaquatic bugs occurring along the margins of the sea..(Leptopodomorpha)..2

b. Wings absent; bugs living on the water surface....................(Gerromorpha)..3

2. a. Minute bugs, body length 1-2 mm.; dorsal coloration uniformly dark; wings thickened and lacking visible venation; posterior portion of head with a collar; living interstitially amid coral cobbles................................*Corallocoris aldabrae* Cobben
b. Larger ovate bugs, body length 3-4 mm.; dorsal coloration black with white markings; wings with clearly evident venation in posterior membrane; head lacking a collar posteriorly; living on open rock faces in the intertidal zone...................................
....*Salduncula seychellensis* Brown

3. a. Hind femur short, not exceeding tip of abdomen; small blackish bugs living near shore, often on pools amid coral rubble..................*Halovelia seychellensis* Andersen
b. Hind femur long, greatly exceeding tip of abdomen; larger greyish to silvery bugs, usually found skating on open water...4

4. a. Middle tibia and tarsi bearing long plumes of swimming hairs on inner margins; male fore femur not greatly swollen, lacking teeth...5
b. Middle tibia and tarsi lacking plumes of swimming hairs on inner margins; male fore femur swollen, bearing teeth on inner margin near apex..................................
....*Hermatobates djiboutensis* Coutiere and Martin

5. a. Width of head between the eyes greater than its length; interocular width about 4 times the width of an eye; body usually unicolorous silvery grey, lacking extensive yellow or brownish markings on the thoracic and abdominal venter or on the dorsum of the head; open ocean species..6
b. Width of head between eyes less than its length; interocular width distinctly less than 4 times the width of an eye; body marked with yellow or brownish on the abdominal and thoracic venter, and usually on the dorsum of the head (either as a posteriorly convex crescent-shaped mark or as a broad patch isolating an arrow shaped dark mark centrally); nearshore species..7

6. a. Smaller species, length of male less than or equal to 4.00 mm., length of female less than or equal to 3.80 mm.; male left styliform process not bent upwards, lying horizontally in lateral view; male tergite IX with patches of black bristles on lateral wings...*H. germanus* White
b. Larger species, length of males greater than or equal to 4.40 mm., length of females greater than or equal to 4.00 mm.; male left styliform process bent abruptly upwards, appearing vertical in lateral view; male tergite IX lacking patches of black bristles on lateral ....*H. micans* Eschscholtz

7. a. Foreleg with the length of tarsal segment I longer than or equal to the length of tarsal segment II...*H. alluaudi* Bergroth
b. Foreleg with the length of tarsal segment I distinctly shorter than the length of tarsal segment II..8

8. a. Foreleg with length of tarsal segment I less than or equal to 2/3 the length of tarsal segment II; male left styliform process not bent outward or visible from above...*H. poseidon* Herring
b. Foreleg with length of tarsal segment I greater than 2/3 the length of tarsal segment II; male left styliform process bent outward, visible from above...................
....*H. flaviventris* Eschscholtz

HERMATOBATIDAE

Hermatobates djiboutensis Coutiere and Martin
Fig. 1

Hermatobates djiboutensis Coutiere and Martin 1901. Bull. Mus. Nat. Hist. Paris, 4, ser. 1: 172. Type-locality: Red Sea, Djibouti.

Discussion: This species is widely distributed in the western Indian Ocean, from the Red Sea southward along the east coast of Africa and eastward to Madagascar, the Mascarenes, the Aldabra group, and the Maldives.

Material examined: ALDABRA ATOLL, **Grande Terre**: calm sea 1000 m. offshore of south coast, east of Dune Jean Louis, 9° 27' 94" S, 46° 25' 92" E, 11:30 hrs., sea temp. 28° C., 8 March 1989, CL 8018. **Malabar**: calm sea 1000 m. offshore of north coast between Passe Gionnet and Anse Malabar, 09:00 hrs., high tide, 12 March 1989, CL 8032. **Picard**: reef crest and calm sea offshore of Aldabra Research Station, 13:00 hrs., 9 March 1989, CL 8024. **Polymnie**: calm sea 1000 m. offshore of north coast between Grande Passe and Passe Gionnet, 10:00 hrs., 19 March 1989. COSMOLEDO ATOLL, **Menai**: calm sea offshore off northeast tip, 9° 42' 04" S, 47° 32' 00" E, 16:00 hrs., 27 March 1989, CL 8041.

GERRIDAE

Halobates micans Eschsholtz
Fig. 2

Halobates micans Eschscholtz 1822. Entomographien 1: 107, pl. 2, fig. 3. Type-locality: given as "Im sudlichen stillen Meere und im sudlichen atlantischen Meere" [types presumably in University of Dorpat].
Halobates streatfieldanus Templeton 1836. Trans. Entomol. Soc. London, 1: 230, pl. 22, fig. A.
Halobates wullerstorffi Frauenfeld 1867. K. K. Zool-Bot. Gesell. Wien, Verh., 17: 458, pl. 12, fig. 5.
Halobates inermis Dahl 1893. Plankton-Exped., Ergeb., 2: 6, figs. 4, 5, 7, 8.

Discussion: This pelagic species is widely distributed throughout all the tropical oceans of the world (see Andersen, 1982, pg. 370, fig. 629).

Material examined: ALDABRA ATOLL, **Grande Terre**: open sea 1000 m. offshore of Dune Jean Luis, 9° 27' 94" S, 46° 25' 92" E, 11:30 hrs., sea temp. 28° C., 8 March 1989. COSMOLEDO ATOLL, **Menai**: on calm sea 1000 meters offshore of northeast tip, 18:00 hrs., 27 March 1989. **West North**: calm sea offshore of west side, 18:00 hrs., 27 March 1989, CL 8042. **Wizard**: net tow on calm offshore sea, 7 March 1989, 21:00 hrs., CL 8017. INDIAN OCEAN, **Somali Basin**: 8° 59' 62" S, 48° 33' 28" E, 28 March 1989, on calm sea; 8° 21' 87" S, 49° 32' 23" E, 29 March 1989; 7° 44' 20" S, 50° 26' 39" E, 30 March 1989; 7° 6' 78" S, 51° 20' 75" E, 30 March 1989.

Halobates germanus White
Fig. 3

Halobates germanus White 1883. Voyage Challenger, Rept. Zool., 7 (19): 50, pl. 1, fig. 6. Type-locality: given as "North Pacific Ocean".

Discussion: This pelagic species is widely distributed in the Indian and western Pacific oceans (see Andersen, 1982, pg. 370, fig. 629).

Material examined: ALDABRA ATOLL, **Grande Terre**: open sea 1000 m. offshore of Dune Jean Luis, 9° 27' 94" S, 46° 25' 92" E, 11:30 hrs., sea temp. 28° C., 8 March 1989; sea 1000 m. offshore of Pointe aux Vacoas, 26 March 1989. **Malabar**: net tow on calm sea 1000 meters offshore from Passe Gionnet to Passe Houareau, 12 March 1989, 09:00 hrs., CL 8032. **Picard**: calm sea off Anse Var, 19 March 1989. COSMOLEDO ATOLL, **Menai**: calm sea 500 meters offshore of Johannes Point settlement site, 9° 41' 68" S, 47° 32' 26" E, 13:00 hrs., 27 March 1989, CL 8041. **West North**: calm sea offshore of west side, 18:00 hrs., 27 March 1989, CL 8042.

Halobates flaviventris Eschsholtz
Fig. 4

Halobates flaviventris Eschscholtz 1822. Entomographien 1: 109, pl. 2, fig. 5. Type-locality: given as "Im sudlichen atlantischen Meere", doubted by Herring (1961) [types presumably in University of Dorpat].

Discussion: This elongate silvery species is typically found cruising parallel to the reef crest 500 to 1000 meters offshore. It is widely distributed on islands throughout the Indo-Pacific region, but is unknown from the coast of East Africa. Distant (1913) recorded this species from Port Sudan in the Red Sea, but this distribution has not been subsequently reconfirmed. Polhemus and Polhemus (in press) note that Distant's (1913) records of *H. alluaudi* from Coetivy and the Amirantes likely represent misidentified specimens *H. flaviventris*.

Material examined: ALDABRA ATOLL, **Grande Terre**: open sea 1000 m. offshore of Dune Jean Luis, 9° 27' 94" S, 46° 25' 92" E, 11:30 hrs., sea temp. 28° C., 8 March 1989. **Picard**: net tow 100 meters offshore of rocky coast from Research Station to Grande Passe, 16 March 1989 (USNM). **Polymnie**: in net tow 30 m. offshore of north coast from Grande Passe to Passe Gionnet, 16 March 1989, CL 8034. **Malabar**: net tow on calm sea 1000 meters offshore from Passe Gionnet to Passe Houareau, 12 March 1989, 09:00 hrs., CL 8032 (USNM). COSMOLEDO ATOLL, **Menai**: calm sea 500 meters offshore of Johannes Point settlement site, 9° 41' 68" S, 47° 32' 26" E, 13:00 hrs., 27 March 1989, CL 8041.

Halobates alluaudi Bergroth
Fig. 5

Halobates alluaudi Bergroth1893. Rev. Ent. Caen 12: 204. Type-locality: Seychelles Islands, Mahe, Port Victoria [types in Paris Museum according to Herring (1961)].

Discussion: This large silvery species is a strong skater and typically occurs along rocky seaward shores. The presently known distribution includes the granitic Seychelles and the atolls of the Aldabra group.

Material examined: ALDABRA ATOLL, **Grande Terre**: Anse Mais, 18 March 1989. **Ile Esprit**: rocky shore and mangroves on south side, 24 March 1989. **Ile Michel**: offshore of mangroves on west side, 22 March 1989, CL 8037. **Malabar**: Passe Houareau at Middle Camp, 19 March 1989, CL 8036; net tow on calm sea 1000 meters offshore from Passe Gionnet to Passe Houareau, 12 March 1989, 09:00 hrs., CL 8032; Passe Gionnet, 20 March 1989. **Picard**: rocky islets and mangrove clumps of *Sonneratia alba* at La Gigi, near Passe Femme, 11 March 1989, CL 8027; offshore reef crest at Research Station, 9 March 1989, CL 8024; net tow 100 meters offshore of rocky coast from Research Station to Grande Passe, 16 March 1989; net tow in lagoon from Passe Gionnet to Passe Femme, 20 March 1989. COSMOLEDO ATOLL, **Menai**: calm sea offshore of settlement site at Johannes Point, 27 March 1989, CL 8041. MAHE: L'Islette Bay, Port Glaud, 1 April 1989, CL 8043.

Halobates poseidon Herring
Fig. 6

Halobates poseidon Herring 1961. Pacific Insects, 3: 287, figs. 52-54. Type-locality: Kenya, Mombassa Island, Port Tudor [holotype in British Museum (Natural History)].

Discussion: This small dull colored species is common among mangroves from the east coast of Africa eastward to Aldabra and Cosmoledo.

Material examined: ALDABRA ATOLL, **Grande Terre**: mangrove estuary lined with *Avicennia marina* at upper end of L'Eglise Channel, off Takamaka Arm, 14 March 1989, CL 8031; Abbott's Creek, 23 March 1989; Anse Mais, 18 March 1989. **Ile Michel**: mangroves on west side, 22 March 1989, CL 8037. **Malabar**: Passe Houareau, 19 March 1989, CL 8036; Passe Gionnet, 16 March 1989, CL 8035; Camp Frigate, 20 March 1989. **Picard**: rocky islets and mangrove clumps of *Sonneratia alba* at La Gigi, near Passe Femme, 11 March 1989, CL 8027; Entre Deux, 20 March 1989; Upsidedown Jellyfish Pool, nr. Aldabra Research Station, 9 March 1989, CL 8022; Bassin Lebine, 9 March 1989, CL 8023. COSMOLEDO ATOLL, **Menai**: along sheltered sandy shore lined with *Avicennia marina*, on lagoon side across from Johannes Point settlement site, 9° 41' 68" S, 47° 32' 26" E, 27 March 1989, 10:00 hrs., CL 8041.

VELIIDAE

Halovelia seychellensis Andersen
Fig. 7

Halovelia seychellensis Andersen 1989. Entomol. Scand., 20: 191. Type-locality: Seychelles, Mahe, Belle Ombre.

Discussion: This small blackish species is common amid coral rubble at the base of limestone cliffs. The presently known distribution includes the granitic Seychelles, northern Madagascar, Aldabra and Cosmoledo.

Material examined: ALDABRA ATOLL, **Grande Terre**: mangrove channel at Abbot's Creek, off of Takamaka Arm, 23 March 1989; east side of Passe Houareau, 23 March 1989. **Ile Esprit**: rocky beach with mangroves on south side, 24 March 1989. **Ile Michel**: rocky shore and mangroves on NW coast, 22 March 1989, CL 8037 **Malabar**: Passe Gionnet, 16 March 1989, CL 8035; Passe Houareau, near Middle Camp, 19 March 1989, CL 8036. **Picard**: Bassin Cabri, behind Aldabra Research Station, 9 March 1989, CL 8021; offshore intertidal reef crest at Aldabra Research Station, 9 March 1989, CL 8024; nearshore reef and rocks at Aldabra Research Station, 9 March 1989, CL 8025 . COSMOLEDO ATOLL, **Menai**: rocky shore near Johannes Point settlement site, 9°41'68"S, 47°32'26"E, 27 March 1989, CL 8041.

Microvelia diluta diluta Distant 1909

Microvelia diluta Distant 1909. Ann. Mag. Nat. Hist., ser. 8, vol 3: 500. Type locality: Bengal, Calcutta.

Discussion: A more thorough discussion of this primarily freshwater species will be presented elsewhere in a report dealing with the freshwater Heteroptera of Aldabra. The localities listed below are only those representing salt water habitats.

Material examined: ALDABRA ATOLL, **Picard**: small tidally flooded limestone sinkhole behind Aldabra Research Station, water temp. 27° C., 10 March 1989, CL 8026. COSMOLEDO ATOLL, **Menai**: tidally flooded limestone sinkhole nr. Johannes Point settlement site, 27 March 1989, CL 8041.

SALDIDAE

Salduncula seychellensis Brown
Fig. 8

Salduncula seychellensis Brown 1954. Ann. Mag. Nat. Hist., 7: 855. Type- locality: Seychelles, Mahe.

Discussion: This small black saldid is known from rocky intertidal habitats on the granitic Seychelles, Madagascar, Aldabra and Cosmoledo.

Material examined: ALDABRA ATOLL, **Grande Terre**: intertidal rocks and cliffs at Cinq Cases, 13 March 1989, CL 8030; intertidal rocks and cliffs at Dune Jean Louis, 9° 27' 16" S, 46° 23' 70" E, 24 March 1989, CL 8040. COSMOLEDO ATOLL, **Menai**: intertidal rocks at Johannes Point, nr. settlement site, 9° 41' 68" S, 47° 32' 26" E, 27 March 1989, CL 8041.

OMANIIDAE

Corallocoris aldabrae Cobben
Fig. 9

Corallocoris aldabrae Cobben 1987. Rev. Zool. Africaine, 101: 24. Type- locality: Aldabra Atoll, Northeast Channel, Middle Island [= Passe Houareau, Malabar Island].

Discussion: This tiny species is known only from the Passe Houareau on Aldabra atoll.

Material examined: ALDABRA ATOLL, **Malabar**: rocky beach north of Middle Camp, Passe Houareau, 22 March 1989, CL 8036.

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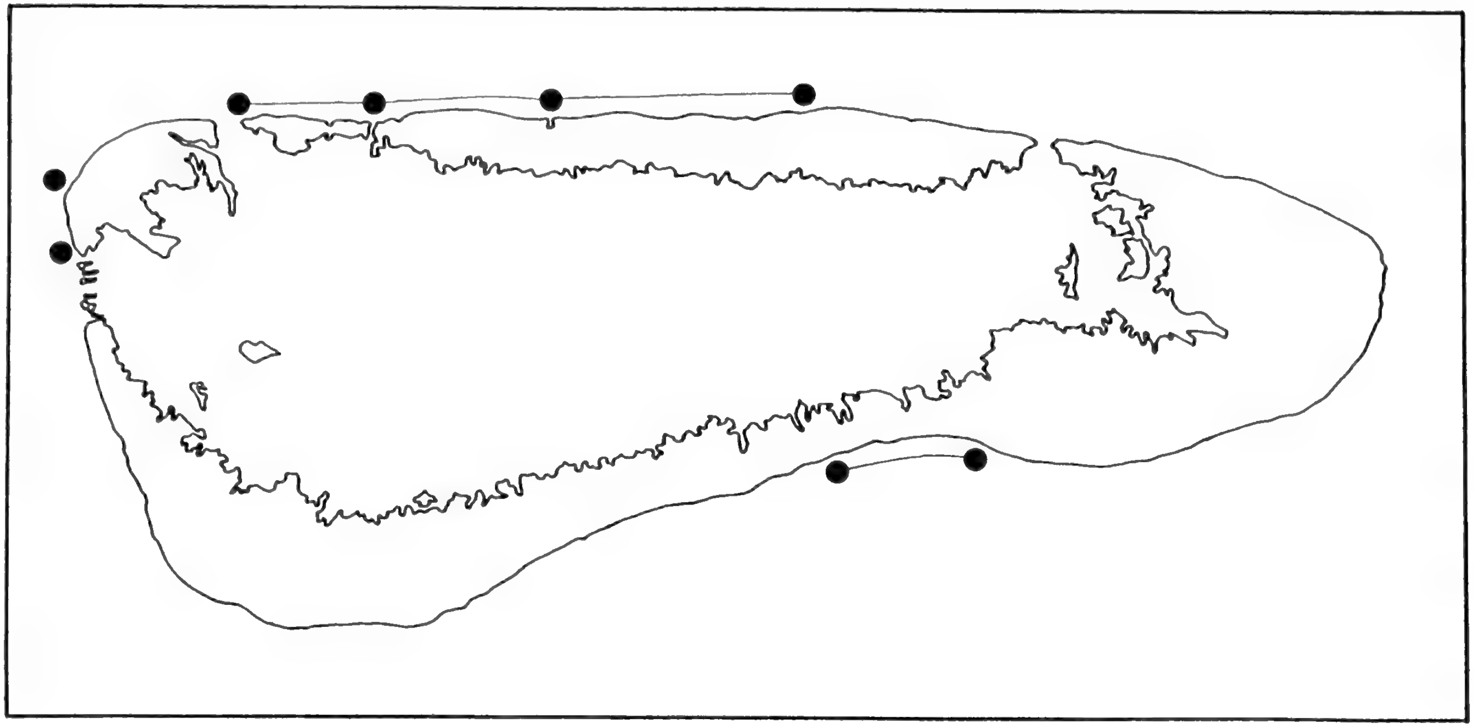

Figure 1. Distribution of *Hermatobates djiboutensis* at Aldabra atoll. Dots connected by lines indicate net tows.

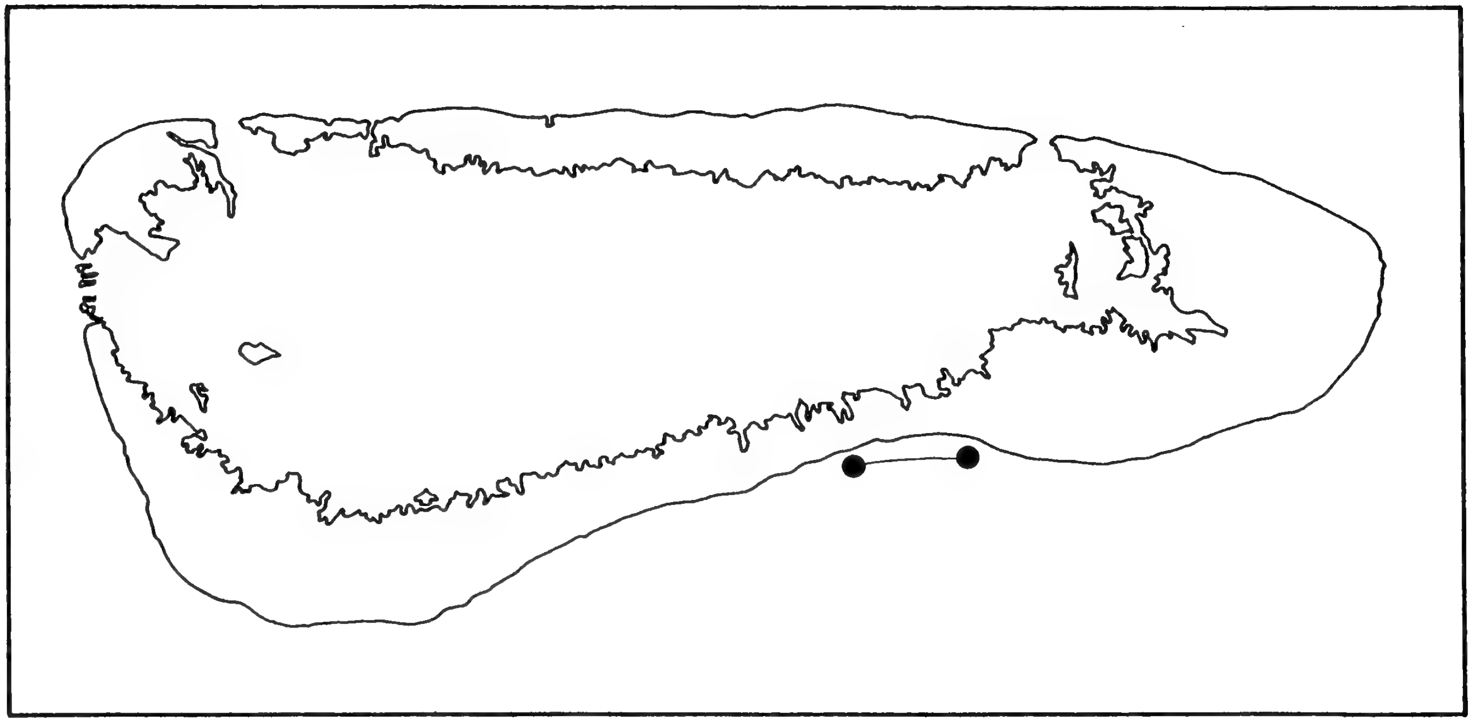

Figure 2. Distribution of *Halobates micans* at Aldabra atoll. Dots connected by lines indicate net tows.

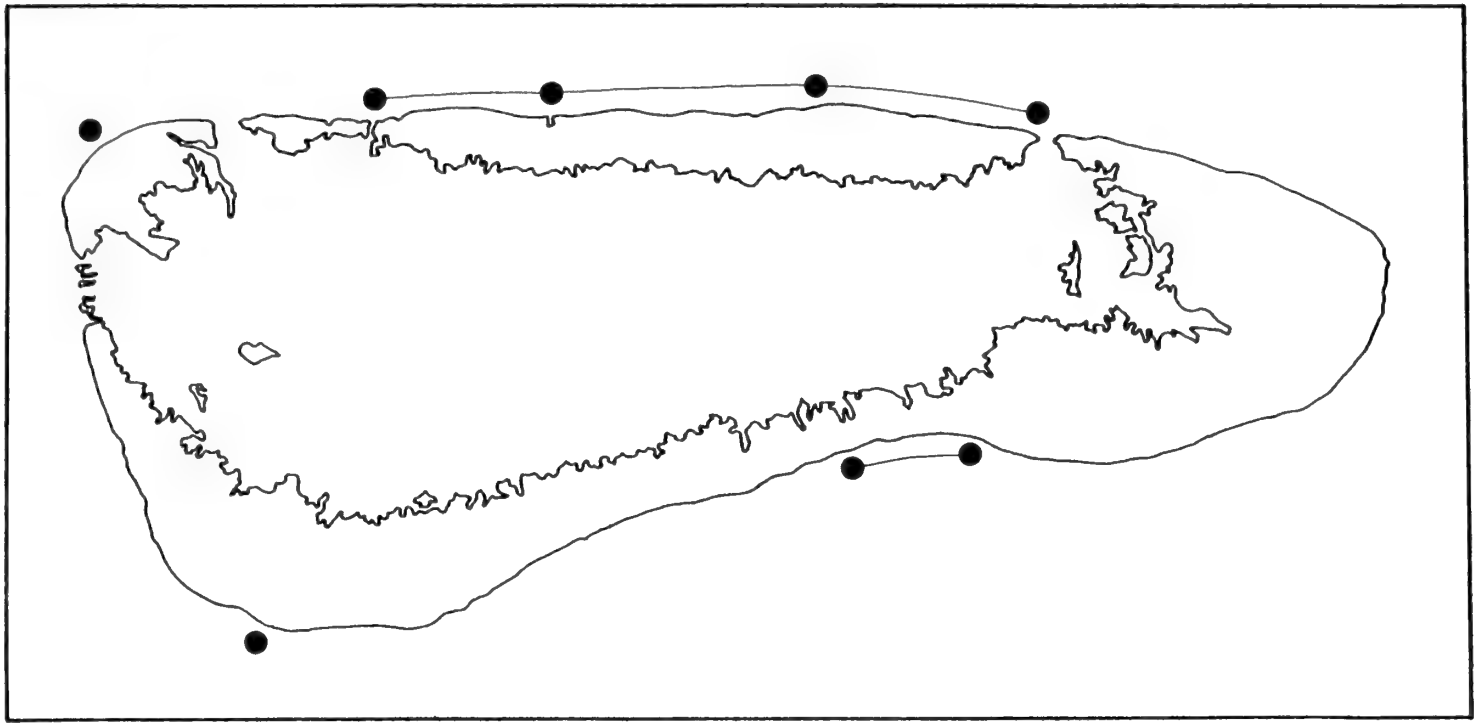

Figure 3. Distribution of *Halobates germanus* at Aldabra atoll. Dots connected by lines indicate net tows.

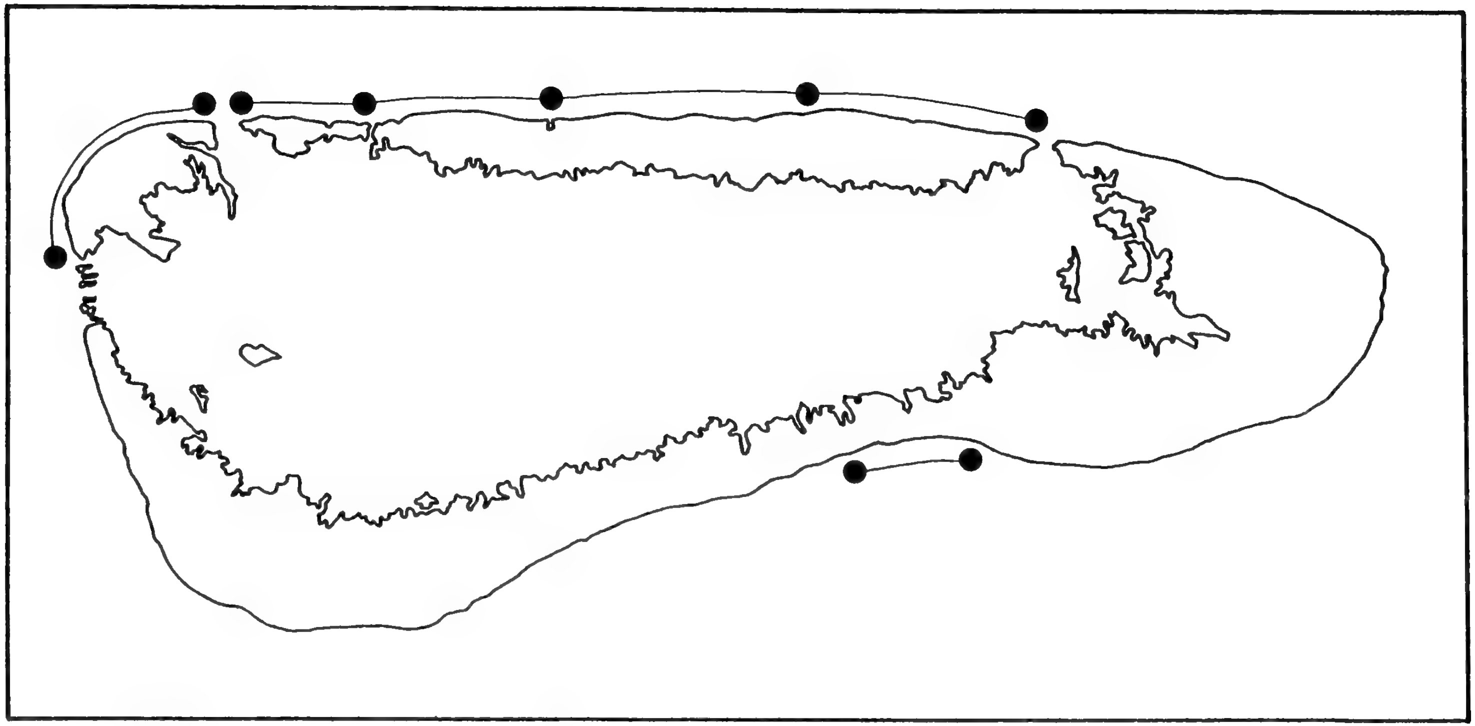

Figure 4. Distribution of *Halobates flaviventris* at Aldabra atoll. Dots connected by lines indicate net tows.

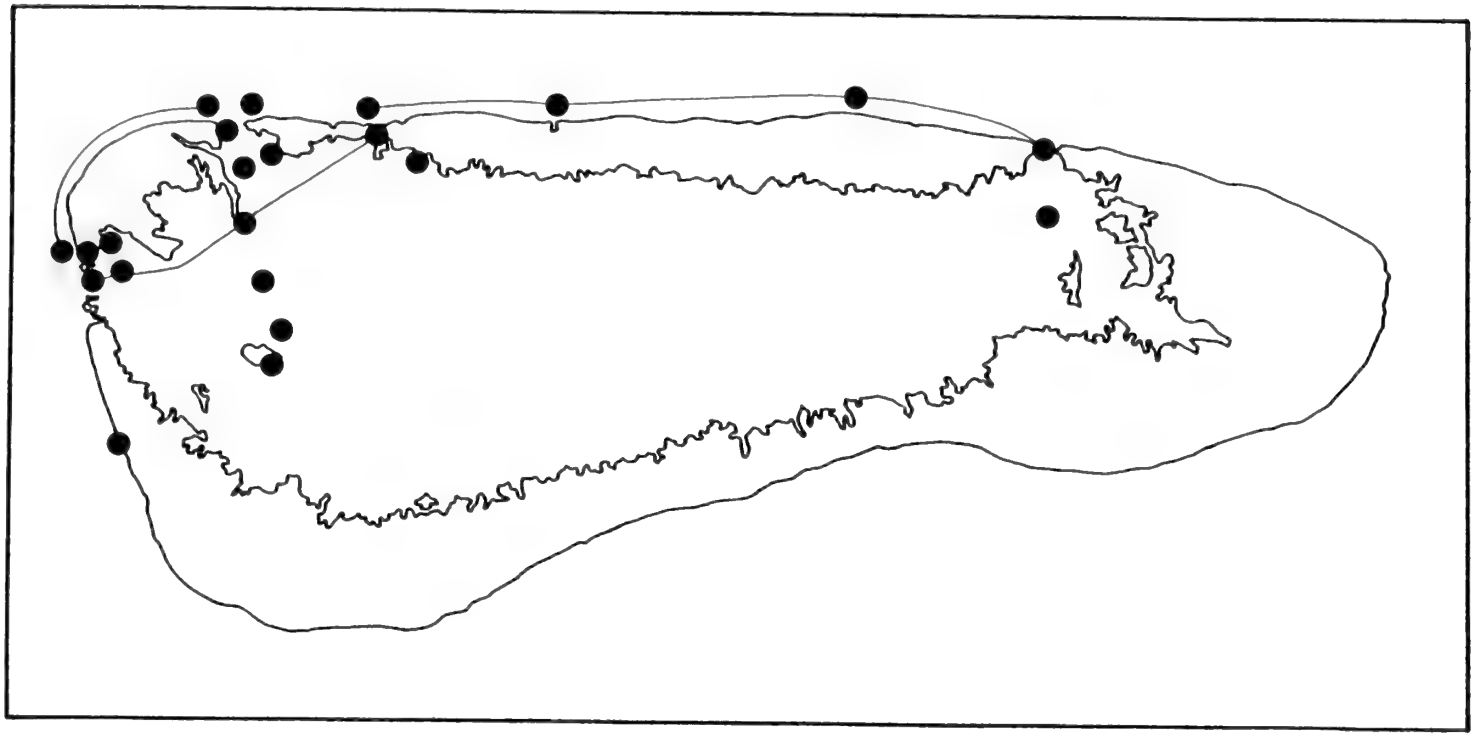

Figure 5. Distribution of *Halobates alluaudi* at Aldabra atoll. Dots connected by lines indicate net tows.

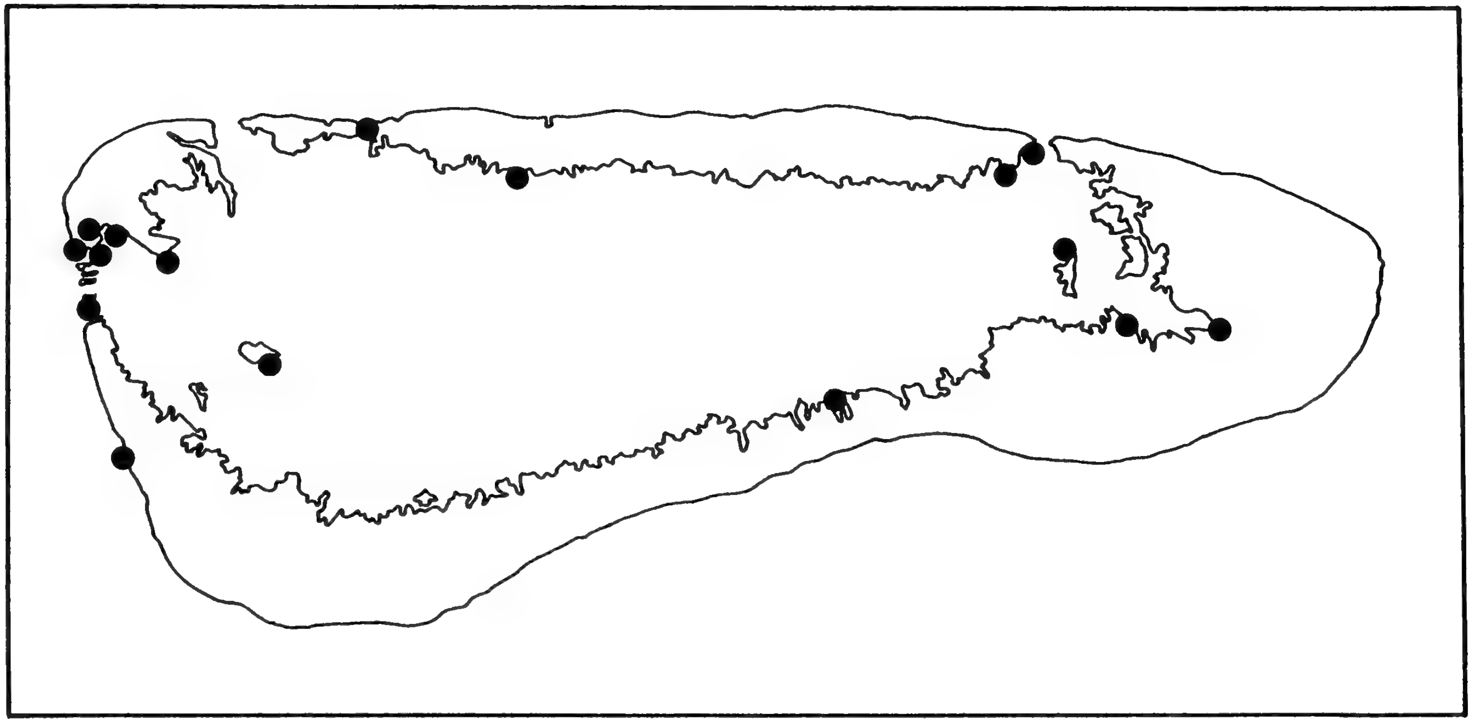

Figure 6. Distribution of *Halobates poseidon* at Aldabra atoll.

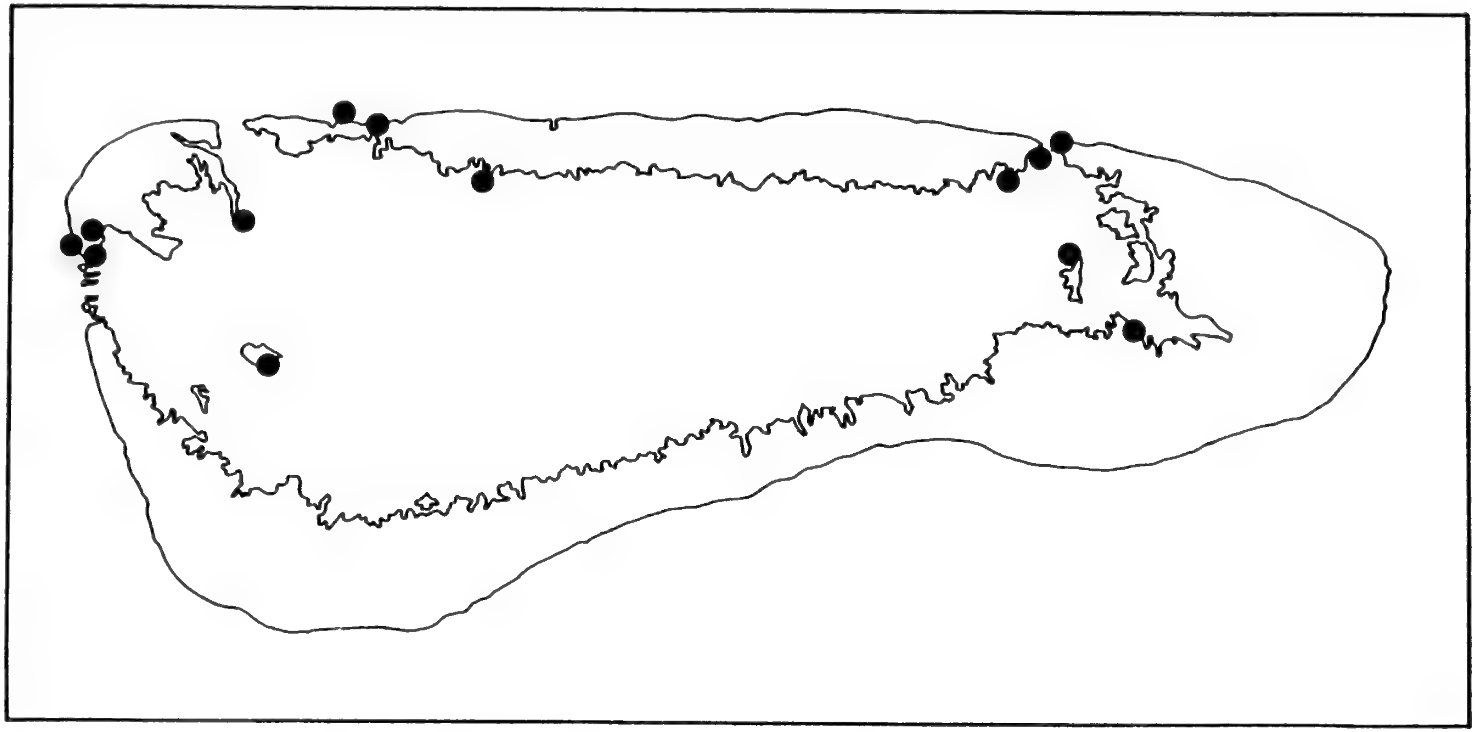

Figure 7. Distribution of *Halovelia seychellensis* at Aldabra atoll.

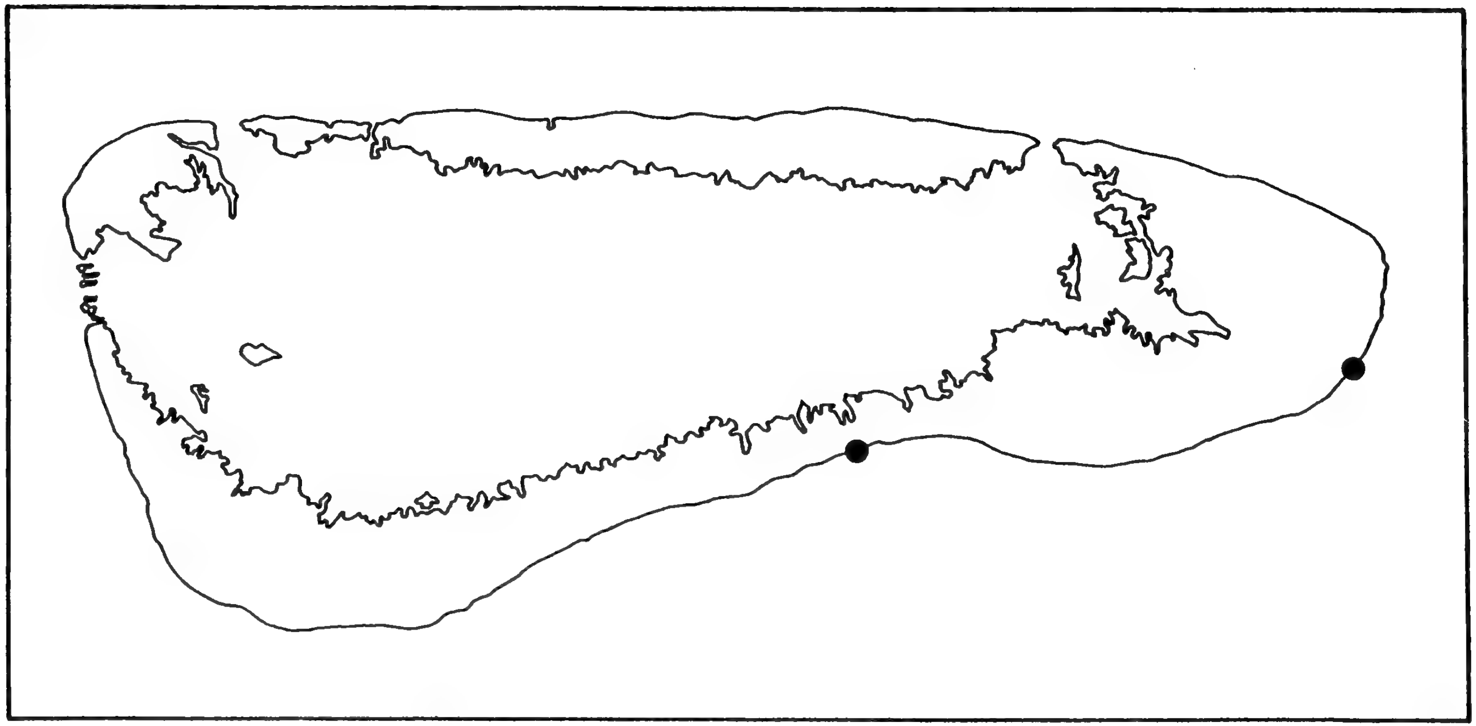

Figure 8. Distribution of *Salduncula seychellensis* at Aldabra atoll.

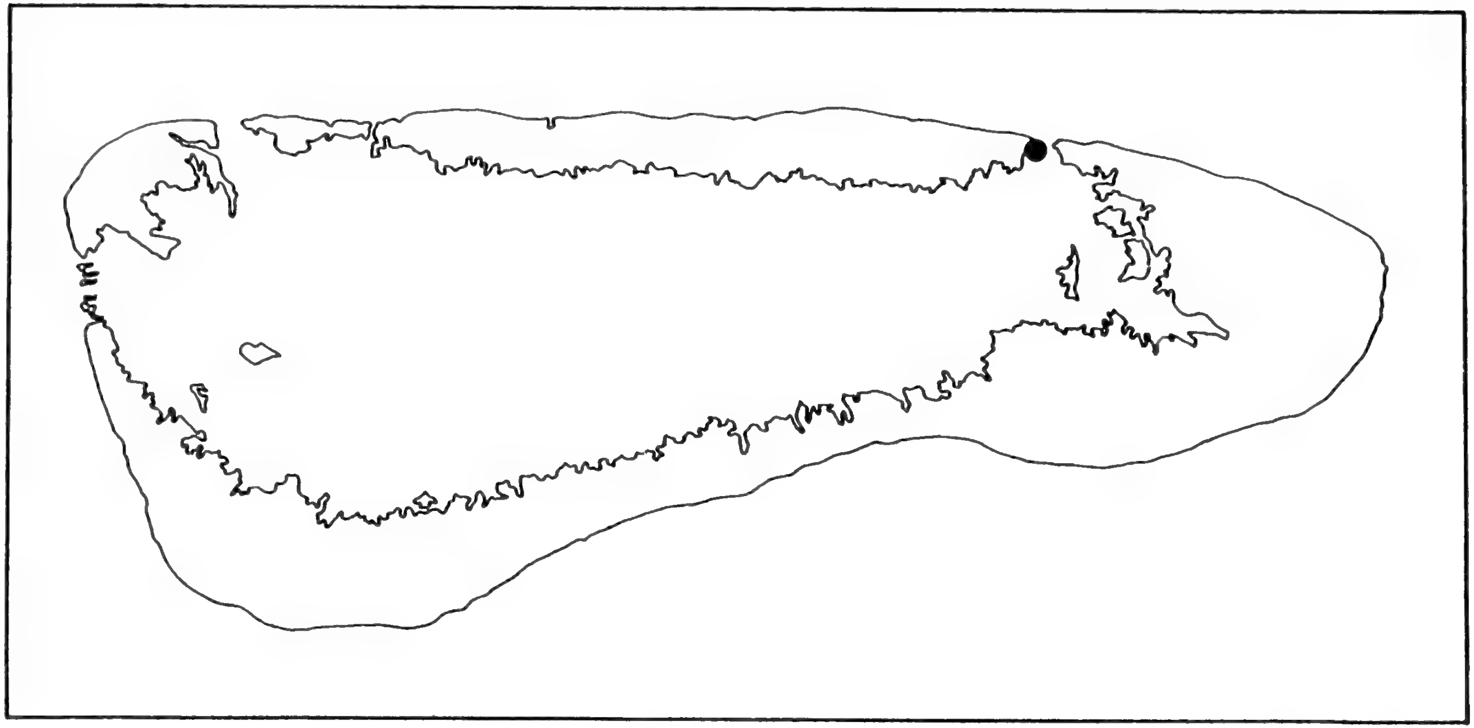

Figure 9. Distribution of *Corallocoris aldabrae* at Aldabra atoll.

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SEDIMENTARY CHARACTERISTICS OF CORAL REEFS IN THE NORTHERN PART OF THE SOUTH CHINA SEA

BY

WANG GUOZHONG, LU BINGQUAN AND QUAN SONGQING

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SEDIMENTARY CHARACTERISTICS OF CORAL REEFS IN THE NORTHERN PART OF THE SOUTH CHINA SEA*

BY

WANG GUOZHONG, LU BINGQUAN AND QUAN SONGQING**

In the northern part of the South China Sea there is a complete range of modern coral-reef types, including fringing reefs, barrier reefs, table reefs and atolls (Fig. 1). The distribution of these coral reefs is controlled either by the terrigenous sedimentation, or by climatic and hydrodynamic conditions. Because of the interference of terrigenous sediments from the Pearl River and other small rivers, fringing and barrier reefs are mainly limited to the Guangdong shelf around Hainan and Weizhou Islands and in some estuaries, such as the estuary Daya near Hong Kong (Wang Guozhong et al 1979, Lu Bingquan et al 1983, 1984). Fringing reefs are absent along most of the coastlines of this continental shelf. Table reefs and atolls are developing off the Xisha Islands area, consisting of more than 30 shoals, banks, islets and islands which cap a submarine platform on the continental slope. Over 1251 m of reef-derived carbonate sediments have accumulated in this area since the Miocene epoch (Fig. 2, Wang Congyou 1979).

The northern area of the South China Sea falls within the tropical biogeographic zone, which extends from about 15° N to 23° N, and for most of the year is dominated by the northeasterly monsoons; in summer, however, typhoons and hurricanes strike from the southwest (Fig. 3). The climate is humid with moderate evaporation. The average water temperatures range seasonally from 20℃ to 30℃, but locally the minimum water temperatures fall appreciably to 18℃ in winter. Salinities over the reefs range from 33.5‰ to 34.0‰. During most of the year the surface water currents flow from northeast to southwest with a complete reversal during the summer months. The tidal range is about 1-2 m.

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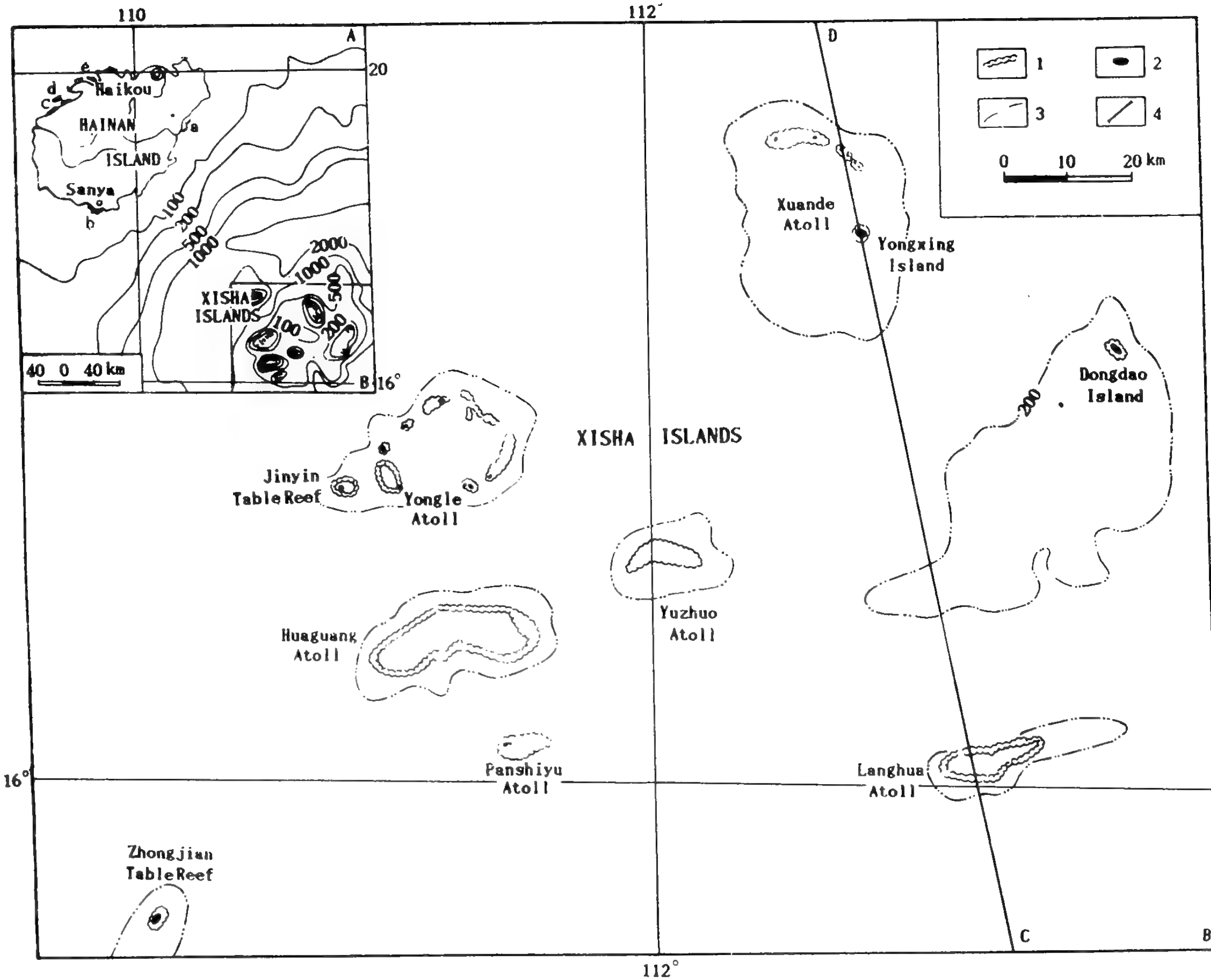

Fig. 1. Distribution of modern coral reefs in the northern part of the South China Sea. Contour depths in meters.

1—Contour of reef crest, 2—Sand cay, 3—200 m isobath, 4—Location of the C—D cross section (see Fig. 2), a—Shalao fringing reef, b—Luhuitou fringing reef, c—Paipu fringing reef, d—Dachan barrier reef, e—Linchang barrier reef (Hainan Island)

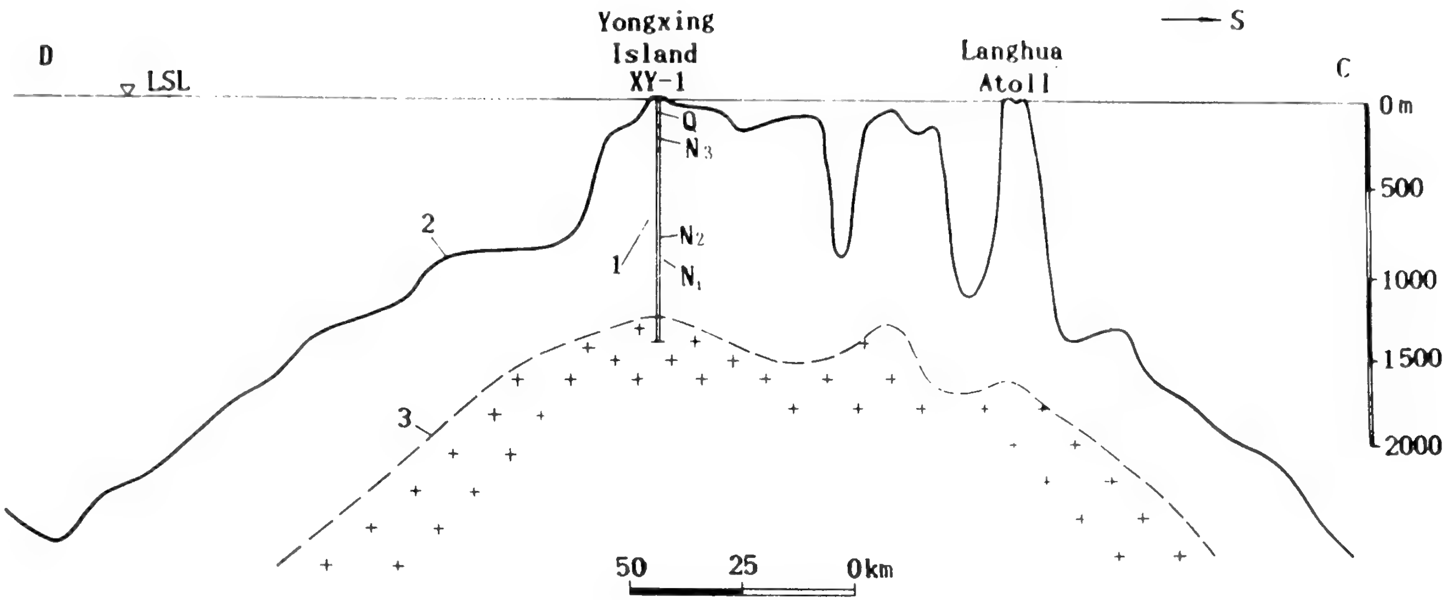

Fig.2. North-South (C-D) cross section of Xisha coral reefs (for location, see Fig.1.).
1—Well XY-1: -- N_1—Miocene(951 m), N_2—Pliocene(150 m), Q—Quaternary(150 m, included Holocene 22 m); 2—Submarine surface; 3—Residuum profile of Neogene system.

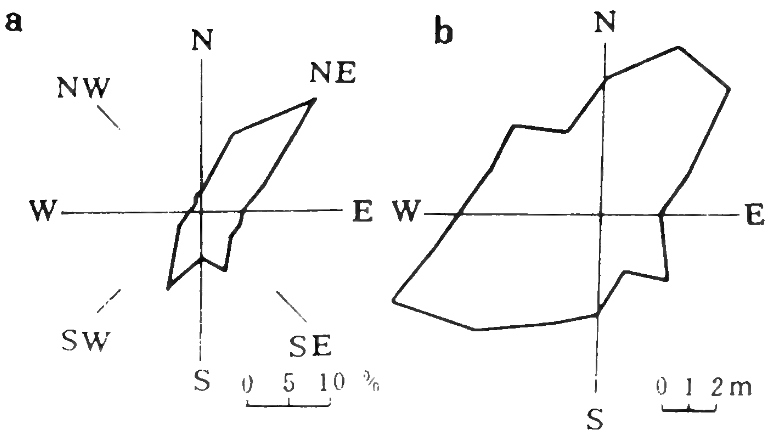

Fig. 3. The wind-rose diagram (a), and distribution of maximum mean wave heights (b) of Yongxing Island

SEDIMENTARY FACIES MODEL OF CORAL REEFS IN THE SOUTH CHINA SEA

Our investigation of the various types of modern coral reefs in the South China Sea revealed consistent zonation pattern for the reef-derived sediments, which are controlled by similar hydrological, geomorphological, biological and sedimentational parameters in this region (Wang Guozhong et al 1982, 1986). There are 7 main sedimentary facies, which are described from the fore reef shoreward as follows (Fig. 4):

The sublittoral sand-mud facies (1) is situated seaward of reefs with a smooth submarine morphology. Its upper limit starts at a depth of 10 m in the Hainan reef area and at more than 20 m in the Xisha reef area. The sediments consist mainly of clastic sand, silt, and muddy silt with patches of carbonate mud. In the Xisha reef area, this zone is almost entirely covered by white biogenic sand with scattered coral shingles, and contrasts with the Hainan and Weizhou reef areas, where the sediments consist of dark

silt and muddy silt, which contain more organic materials and terrigenous particles. The sea floor in this facies is often covered with the mounds of burrowing organisms and grasses. In this zone, there are many ostracodes and foraminifera, and the proportion of planktonic foraminifera, such as Globigerina, increases gradually seaward.

The fore-reef talus facies (2) extends from the lower limit of coral growth, which is about 5 m in the Hainan reef area and over 20 m in the Xisha area. The width of this zone ranges from 10 to 90 m. The slope is steep in the upper limits and becomes more gentle at the bases. Sediments of this facies range from boulders to sand. Living scleractinian corals are generally not found in this zone which is characterized by red algae, some gorgonians, gastropods and echinoids.

The autochthonous reef facies (3) extends from the edge of the reef flat, or low tidal level to the lower limit of coral growth as mentioned above. Its width generally ranges from 20 to 200 m and reaches a maximum of 500 m. The reef face is a slope with gradients from 6° to 30° . In this interval there are two terraces at depths of about 5 m and 10 m, which are thought to be eustatic topographic features formed during lower stands of sea level. There are 3 spur and groove (buttress) systems (Fig. 5). Two of them consist of closely-spaced, steep-sided linear highs and lows, that extend perpendicularly seaward from the reef flat; the third system with steep sides 2 m in breadth and 1-3 m in depth extends around the reef margin i.e. parallel to the reef front in ten -m lengths in water depths of about 10 m. The groove sections are both V-type and U-type and have a relief of less than 2 m. The origin of the grooves in the investigated regions is mainly erosional (Fig.9) with some constructional features.

The area covered by living coral communities on the reef face may reach 70-90% , while the rest is occupied by algae and sediments. The scleractinian corals in the coral growth zone can be grouped into two broad coral communities. The shallower (upper subzone) communities are dominated by branching and encrusting corals, such as Acropora, Pocillopora, as well as Millepora (Fig. 10,11) and coralline algae, while the deeper (lower

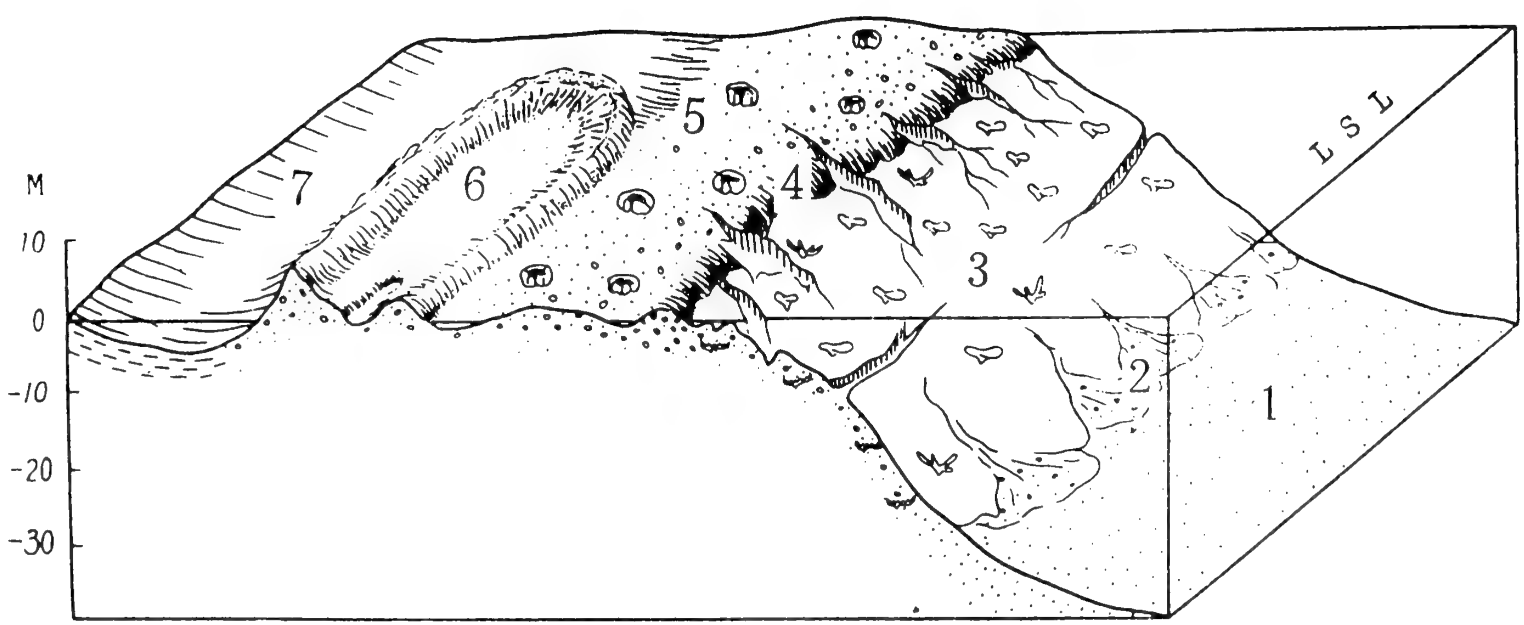

Fig.4. Sedimentary facies model of coral reefs in the northern part of the South China Sea.

1- The sublittoral sea sand-mud facies; 2- The fore-reef talus facies; 3- The autochthonous reef facies; 4- The marginal reef conglomeratic (boundstone) facies; 5- The reef flat sandy-gravel facies; 6- The sand cay gravel-sand facies; 7- The lagoonal sand-silt facies

subzone) communities contain mostly plate-like and foliose corals such as Acropora corymbosa, Acropora surcolosa and Pavona (Fig. 12). The hemispherical and massive coral species such as Porites and Favia are minor components of both subzones.

Many skeletons and shells of various organisms that grow in this facies are broken by wave action and transported mostly to the fore- and back-reef areas. Therefore, this zone becomes the source of most of the reef-derived sediments. The rigid reef framework, produced mainly by hermatypic corals, is filled with debris of various organisms and is cemented by coralline algae and by interstitially precipitated carbonate.

The marginal reef conglomeratic (boundstone) facies (4) is situated at the margin of reef flat in the form of small mounds 0.3-1 m above low tide level (Fig. 13), or rarely as gravel dams about 5 m above low tide, such as in the northwest of Hainan island, formed in response to a greater tidal range. Depending on the hydrodynamic conditions, reef margins may consist of pure gravels of reef materials or boundstones (Fig.14) and algal ridges formed by crustose coralline algae (such as Porolithon, Hydrolithon and Neogoniolithon) under conditions of very high wave energy. These algal ridges are common off the northeast margins of some islands of the Xisha Islands (as Dongdao Island, Jinyin Island etc. Zhuang Qiqian et al 1981).

The reef flat sandy-gravel facies (5). The reef flat is a broad and flat geomorphological element near low tidal level with a central prominence, which is exposed above low tidal level. Its width generally ranges from 20 to 200 m, and the maximum width reaches about 1000 m. In the Xisha Islands, because of the influence of the asymmetrical monsoons, the northeastern reef flats are wider than the southwestern, and the outer parts of atolls are wider than the inner parts (Fig. 6 and 7, Wang Guozhong et al 1986). The floors of the flats consist of sandy-gravel sediments with abundant coral patch reefs. From the reef margin shoreward the sorting and sphericity of the debris increases. Water depths on the reef flat control the development of living coral communities and other reef habitat organisms. These coral communities are sparse in some places, abundant in others, sometimes covering more than 50% of the reef flat. Heights of coral communities

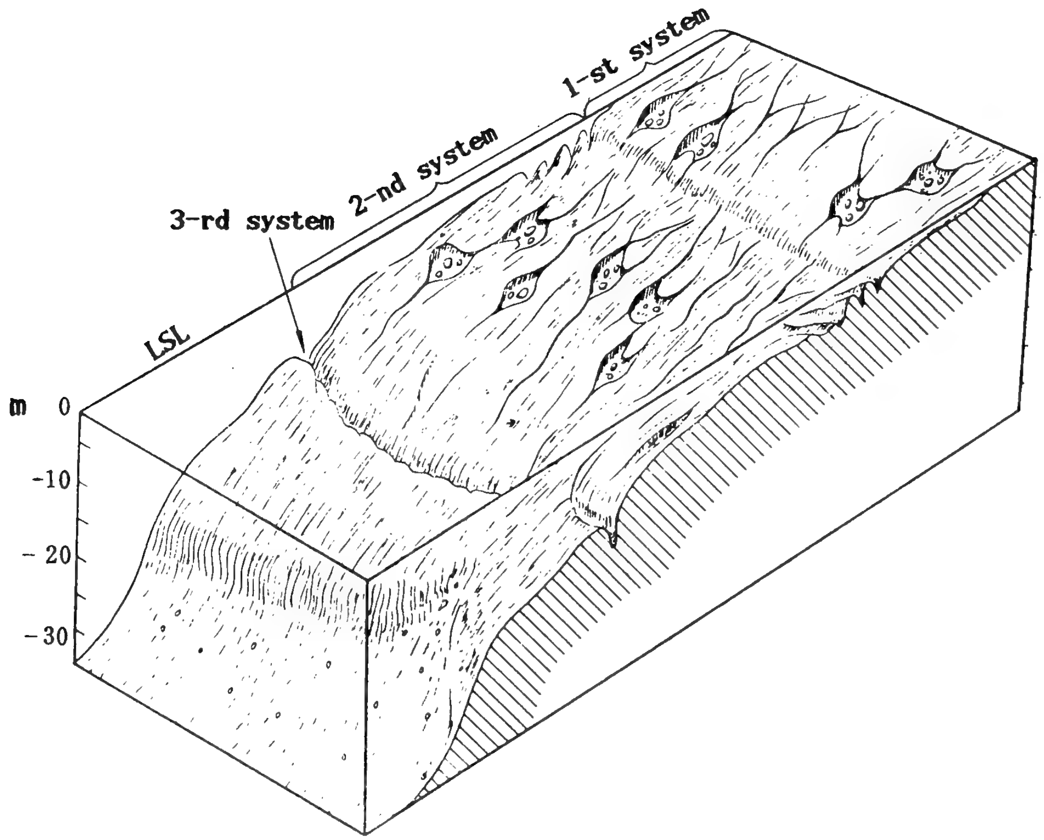

Fig. 5. The spur and groove systems of the autochthonous reef facies southwestward of Yongxing coral reef

range from 0.3 to 1 m. Coral species are dominated by encrusting, branching, plate-like (microatoll) and hemispherical corals. Scleractinian corals include Acropora (Fig.15), Montipora, Porites and Favia. In the Xisha Islands there are microatolls of Heliopora (Fig.16) and encrusting Tubipora amongst octocorals, a characteristic feature of Indo-Pacific reef flats (Milliman 1974). The variety of biota on the flats in the South China Sea is remarkable. The reef habitat organisms include mollusca, ostracoda, echinodermata, sponges, foraminifera, along with numerous algae dominated by Halimeda and Udotea. All 6 species of Tridacnidae (Fig. 17) are present, which is another characteristic feature of Indo-Pacific areas (Zhuang Qiqian, et al 1978). Benthonic foraminifera grow profusely and form 91.6-96.9% of the foraminiferal assemblage, which is dominated by Calcarina sp. and Amphistegina sp. (Wang Guozhong 1986).

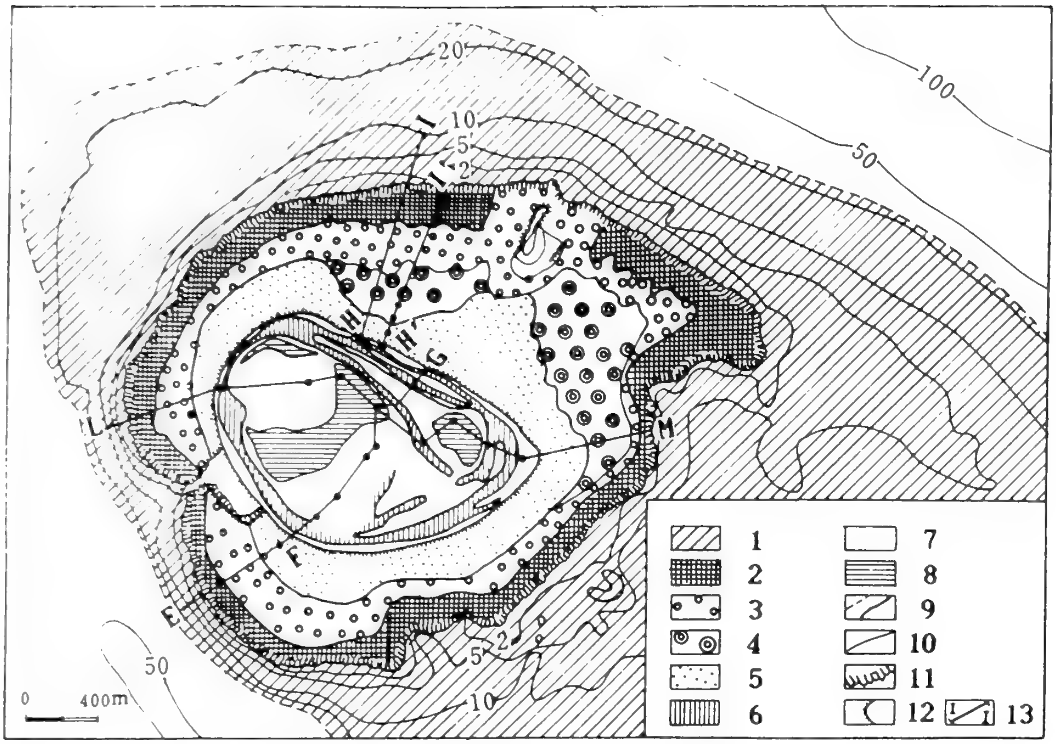

Fig. 6. Distribution of sedimentary facies of Yongxing table reef.
1- The autochthonous reef facies; 2- The marginal boundstone facies; 3-5 The reef flat facies; 6-8 The sand cay facies; 9- Boundary line of facies; 10- Isobath; 11- Reef margin; 12- Coast line; 13- Cross section.

The sand cay (barrier) gravel-sand facies (6). In the Xisha area, sand cays are built up on southwest areas of the reef flats, in response to the dominant influence of the northeast monsoon winds. Lengths and widths of cays generally range from 20 to 200 m and the longest reaches over 1900 m. In fringing reef areas off Hainan Island the sand cays develop into sand barriers or coastal sand dams. Sand cays occur in high energy environments with sand and gravel beaches on their seaward slopes. In the supratidal zone there are 1-4 rows of barriers or dams and dunes. These storm ridges have a relief of 1-2 m and are covered with 5-6 m of vegetation (Fig.18) . The central cay areas consist of sand-gravel flats, depressions and lagoons

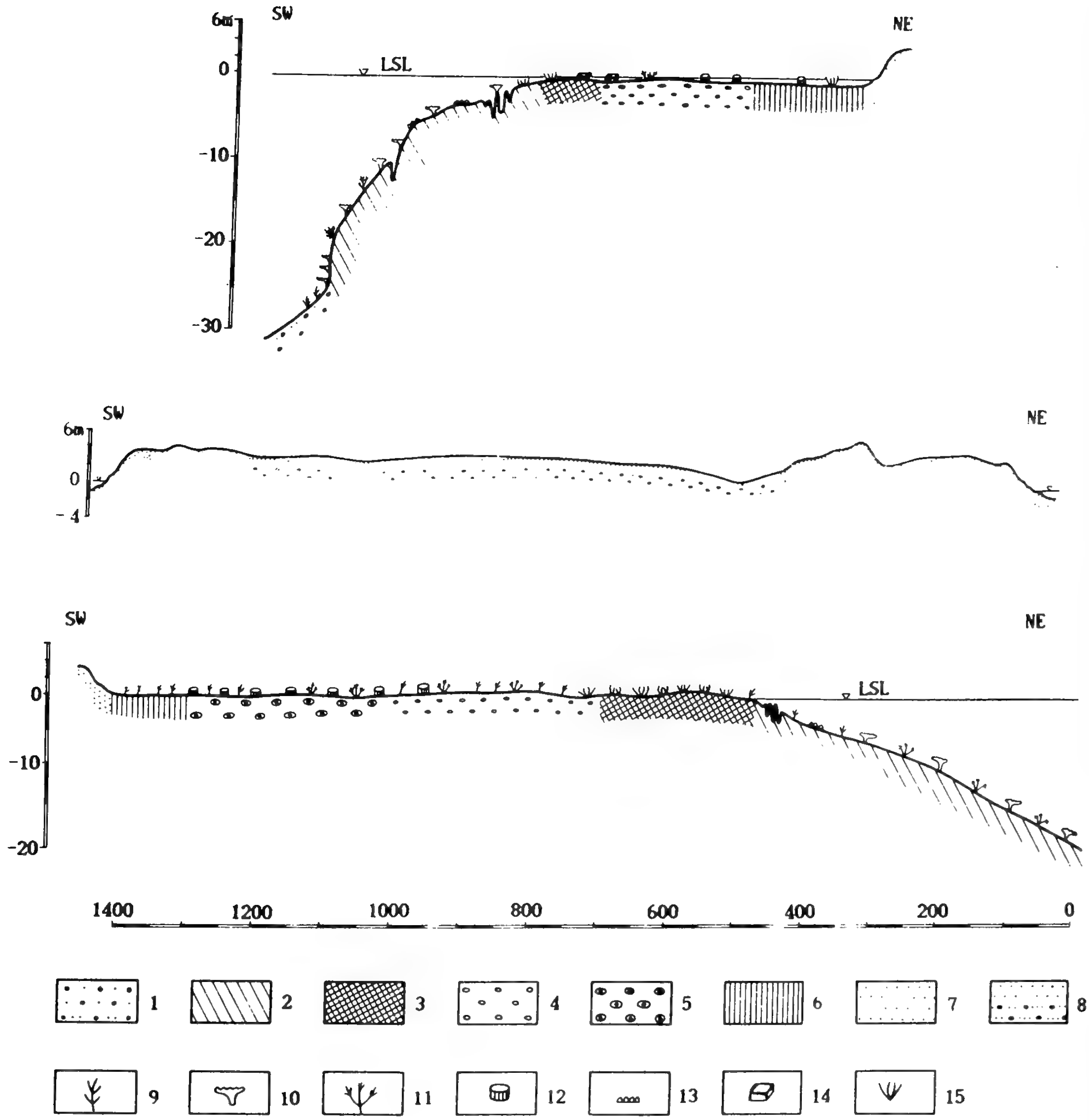

Fig.7. Cross sections of sedimentary facies across the Yongxing table reef (for location, see Fig.6).

1- The fore-reef talus facies; 2- The autochthonous reef facies; 3- The marginal reef conglomeratic (boundstone) facies; 4- The reef flat gravel facies; 5- The reef flat microatolls of Heliopora and Porites facies; 6- The reef flat sand facies; 7- The Sand Cay gravel-sand facies; 8- The Sand Cay flat and depression facies; 9- Gorgonian 10- Plate-like corals; 11- Branching corals; 12- Corals with microatoll form; 13- Short branching corals; 15- Algae.

(coastal lagoons), which are both brackish and hypersaline with salinity 7.33 to 50.76‰.

The carbonate sediments of these sand cays consist, for the most part, of debris from coral skeletons and molluscs with a marked increase in foraminifera and algae debris in the finer size fractions (Fig. 8). Some islands of Xisha area have guano deposits. Sometimes sand cay sediments are lithified which assists stabilizing sediment migration.

The lagoonal silty-sand facies (7). Lagoons are located in atolls, faros and at the back of fringing reefs. Depths of the majority of lagoons are generally less than 10 m, but some large lagoons may reach over 50 m. Sediments on the lagoonal slopes are mainly carbonate sand with coral debris or shingles. Patch reefs within the lagoons have mound-like and linear forms and, for the most part, consist of symmetrical conical coral zonation

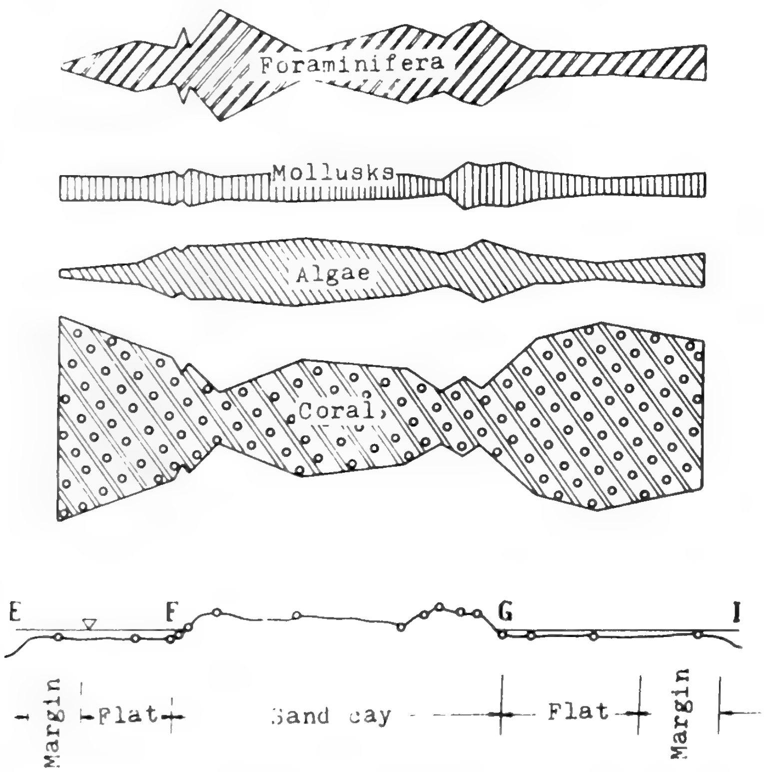

Fig. 8. Distribution of sand-size components of Yongxing coral reef along cross sections E-F-G and H-I (for location, see Fig.6)

that includes bush-like corals, such as Pavona sp., Pocillopora sp. , Acropora sp. , Fungia sp., Alcyonaria etc. The lagoon floors generally consist of sand and silt characterized by poor sorting, and the overlying waters are rich in suspended sediment but on some lagoon floors, even at depths of 30-50 m many encrusting corals grow, including Montipora foliosa, and Galaxea sp. Along with abundant sponges, the percentage by living coral cover may reach more than 80% (Huaguang Atoll).

Lagoon sediments contain well-preserved bivalves with thin shells, and the foraminifera are dominated by benthonic forms with porcelaneous tests.

CORAL AND SEDIMENTARY CHARACTERISTICS

Hainan and Weizhou reef areas located on the Guangdong shelf, belong to the category of shelf reefs. The table reefs and atolls in the Xisha reef are established on a submarine platform on the continental slope and may be compared with oceanic reefs, but have their own characteristics (Fig.1).

The South China Sea, as a marginal sea, is located geographically between the Pacific and Indian Oceans and represents a transitional region between them.

As a result of the weaker influence of the Pacific warm current (Kuroshio) and stronger influence of northeast and southwest monsoons, coral reefs in the South China Sea have their own specific features that can be described as follows:

Scleractinian corals of the South China Sea belong to Indo-Pacific coral reef region, but the organism diversities are relatively low. For example, 45 genera and more than 179 species of scleractinian corals are found here (Zou Renlin et al 1983), versus more than 700 species in Indo-Pacific areas and 350 species in the Great Barrier Reef area; however, only 1/3 as many (about 50 species) are found in the Caribbean (Milliman 1974, Reading 1978) (Table 1). In the Xisha area Heliopora and Tubipora (Octocorallia) are well

developed and all 6 species of tridachnidae (mollusca) are found; both are characteristic features of Indo-Pacific reefs (Zhuang Qiqian et al 1981).

Table 1. The organism diversities of coral species in various reef areas

	South China Sea	Pacific* Ocean	Great Bar-* rier Reef	Caribbean* Sea
Species of corals	179	700	350	50
Heliopora	+	+		−
Tubipora	+	+		−

*After Milliman 1974.

Because northeast monsoon winds are stronger than those from the southwest, coral reefs are better developed northeastward than those found southwestward. Coral reef zones in the northeastward areas are wider and have a higher production of carbonate sediments than that found in southwestward reefs (Fig. 6). On the northeast outer-reef flats of some Xisha Islands, crustose coralline algae ridges are developing, but they are weaker than those found in Pacific. In contrast, algal ridges are absent from most Indian Ocean reefs (Tracey et al 1948, Mergner et al 1974, Milliman 1974).

Most Pacific atoll sand cays are located on windward reefs (Milliman 1974) , while many cays of Xisha Islands occur on more leeward areas southwest of the reef flat or on the inner sides of the reef flat of atolls. Since most reef flats lack algal ridges, this leeward position of sand cays is more similar to that found in Indian Ocean reefs (Milliman 1974).

The composition of reef and lagoonal carbonate sediments can well reflect the environment of deposition, the distribution of populations, and productivities of the various organisms, which in turn, are influenced by the climate, current system and hydrodynamic regimes. As products of high energy environments, the shallow-water reef derived sediments of the South China Sea generally consist of coarser debris, such as sand and gravel, with an absence of lime-mud as well as oolites and cemented carbonate grains.

With respect to the total sediments, coral skeletal detritus and skeletons are the dominant component and constitute from 21 to 85% of the total sediment. Algal fragments are relatively unimportant, constituting only 3 to 27% of the sediment (Fig. 7, Tables 2, 3). This sediment distribution is more analogous to that found in the Australian Great Barrier Reef in contrast to that associated with coral reefs in the areas of Indo-Pacific and Caribbean, which are predominantly composed of algal debris ranging from 12 to 64%. Benthonic foraminifera are major contributors to both the South China Sea, or Indo-Pacific reef-flat sediments, which contrasts with their paucity in Caribbean reef sediments (Ginsburg 1965, Milliman 1974, Reading 1978). The quantities of molluscan fragments found in various reef areas are similar but the ratio of molluscan to algal debris can be indicative of biological areas. For example, this ratio in the South China Sea is more than 0.5, but in the other reef areas it is less than 0.5 (Table 3).

To summarize, because of their location between Pacific and Indian Oceans, the sedimentology of coral reefs in the South China Sea represents a transitional pattern which has a closer similarity to sedimentary characteristics of the Great Barrier Reef.

Table 2. Composition of the sand-size components of reef flat sediments from various reef areas

	South China Sea	Pacific* Ocean	Caribbean* Sea
Coral	21-85	15-36	20-35
Algae	3-43	25-62	12-64
Foraminifera	1-21	10-23	2-13
Mollusk	5-19	12	5-22
Mollusks/Algae	0.93	0.28	0.36

*After Milliman 1974.

Table 3. Composition of the sand-size components of lagoonal sediments from various reef area

	South China Sea	Pacific* Ocean	Caribbean* Sea
Coral	40-69	15-36	25-35
Algae	7-35	33-54	41-53
Foraminifera	6-8	10-23	2-3
Mollusk	15-17	10-12	5-15
Mollusks/Algae	0.65	0.25	0.21

*After Milliman 1974.

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Figure 9. The groove with U-type section shows the erosional origin; bottom covered by white biogenic sand.

Figure 10. The shallower community consists of branching corals, dominated by Acropora sp.

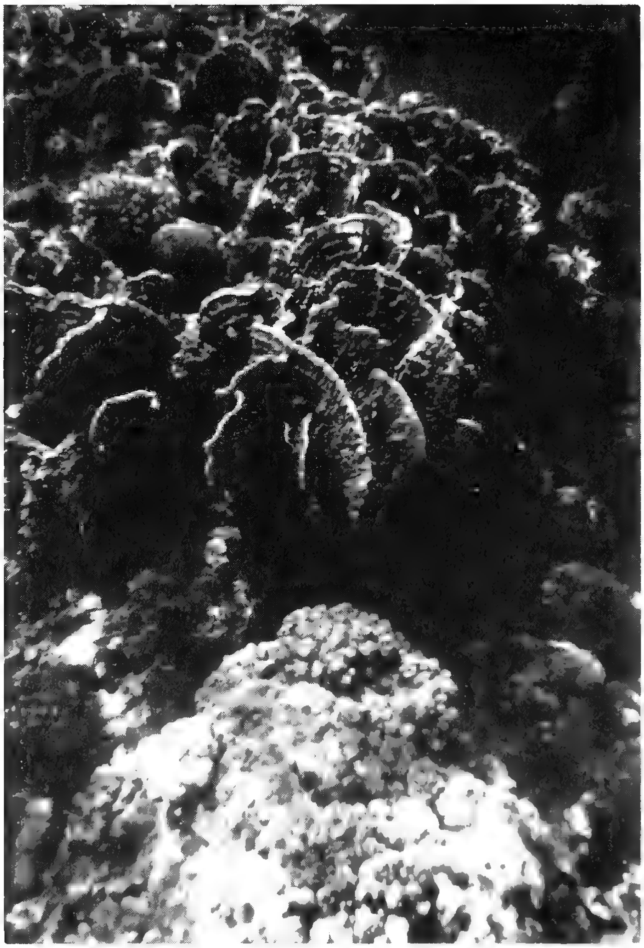

Figure 11. The shallower water hermatypic organisms -Millepora, Pocillopora etc.

Figure 12. The scleractinian corals-Acropora corymbosa, Acropora pacifica etc.

Figure 13. The view of the reef margin.

Figure 14. The reef margin consists of reef rocks and gravels; floor consists of bound-stones.

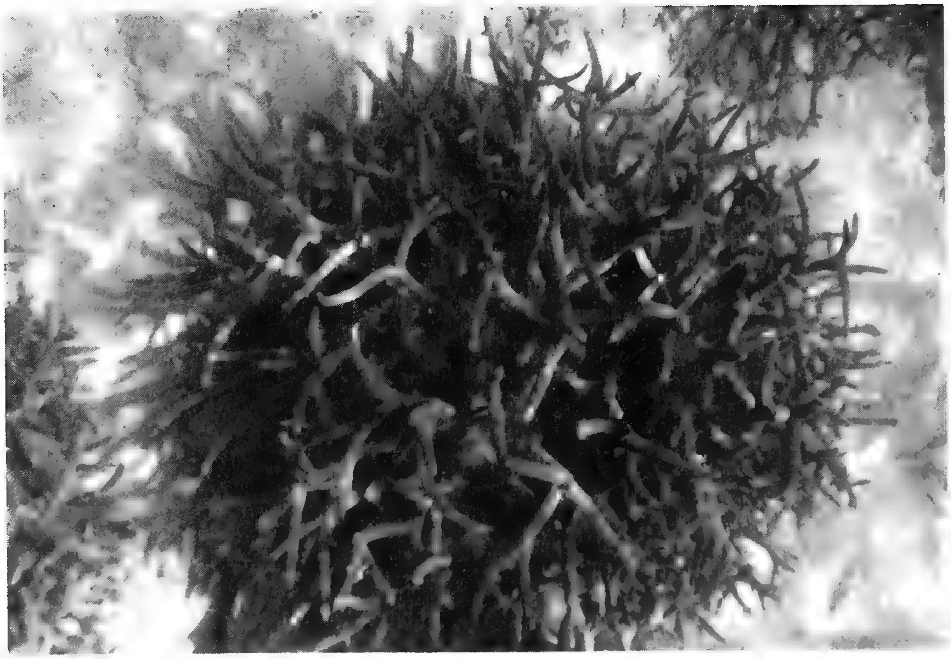

Fig. 15. The bush-like corals - Acropora sp. on the reef flat.

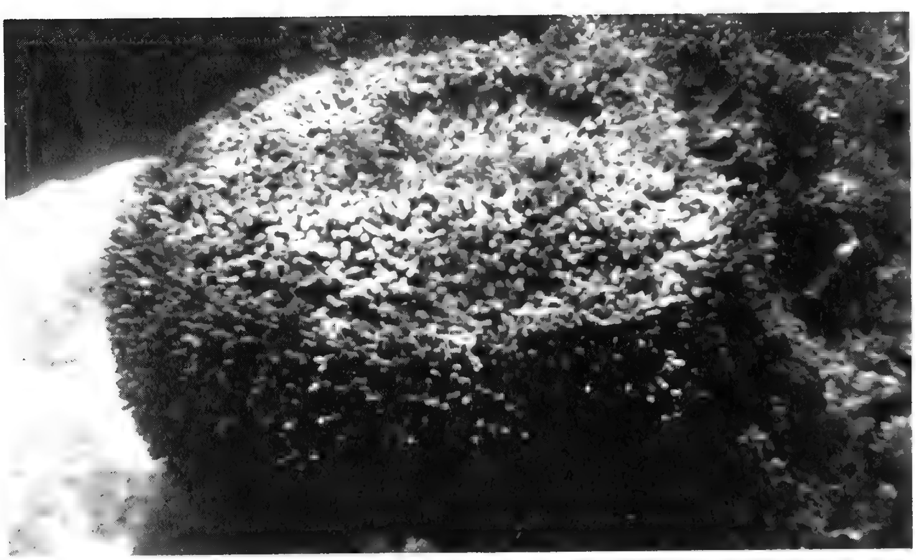

Fig 16. The microatoll of Heliopora - a species of octocorals on the reef flat.

Figure 17. The tridacnid is living on the reef flat of the South China Sea.

Figure 18. The dune, with vegetation of Scaevola sericea, 5-6 m in height.